

Intra-annual variations in climate influence growth and wood density of Norway spruce

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Summary Intra-annual radial growth variations of two Norway spruce trees (*Picea abies* (L.) Karst.) were monitored over 4 years, at four heights up the stem, by means of point-dendrometers. The trees were then felled and radial wood samples were cut from the radii that had been monitored by the dendrometers and analyzed for density. From the radial growth measurements recorded by the dendrometers, we related positions within the rings to dates, thus making possible investigation of the relationships between changes within the rings in wood density and fluctuations in climate or growth rate. Radial growth started in early April and ended, with large intra-annual differences, in August or September. Short-term variations in growth rate were related to fluctuations in climate parameters and soil water reserves. The sensitivity of radial growth to climate decreased with stem height. Wood density responded strongly to drought events, and a dry period in June 1996 induced false-ring formation. Wood density was relatively independent of growth rate and climatic conditions during the first part of the growing season, but increased with decreasing radial growth rate later in the growing season.

Keywords: dendrometer, *Picea abies*, tree ring, water availability.

Introduction

Changes in forest productivity in Europe indicate that forest growth has altered considerably during the past decades (Becker et al. 1995, Spiecker et al. 1996). Global climate simulation studies predict that, in the future, trees in Europe are likely to experience more severe droughts and higher summer temperatures (Cubash et al. 1995, IPCC 2001). These changes could affect not only tree growth, but also wood density (WD) and wood properties, especially in species characterized by large differences between early- and latewood densities. Den-

droclimatic studies have shown that WD is highly sensitive to climate variations at the inter-annual time scale (e.g., Parker and Henschel 1971, Schweingruber et al. 1978). The strength of the relationship between WD and climate has led to the use of WD as a key parameter for climate reconstruction (Hughes et al. 1984, D'Arrigo et al. 1992, Briffa et al. 1995, 1998). However, inter-annual studies to date have considered only WD values averaged over entire annual rings, or of early- and latewood parts of annual rings. Similarly, dendroclimatic studies have focused only on the density of a part of the annual ring, namely latewood, or on maximum density of softwood species. Information from a comprehensive study of the control of wood formation and its dependence on climatic conditions is of major interest because tree physiological processes, wood density and wood properties are interrelated (Deleuze and Houllier 1998).

Decoux et al. (2004) have shown that WD exhibits maximum variability at the intra-ring scale, ranging from about 300 to 1000 kg m⁻³. Relationships between climate and wood anatomy or ring development have been studied at intra-annual time scales in various tree species including black locust (*Robinia pseudacacia* (L., Schmitt et al. 2000), beech (*Fagus sylvatica* L.) (Sass and Eckstein 1995, Schmitt et al. 2000) and Norway spruce (*Picea abies* L. Karst.) (Horacek et al. 1999, Mäkinen et al. 2003). Although these studies provided information on the physiological processes underlying ring formation, from cell division to its enlargement and maturation, they provided little information on the effects of climate on wood anatomy or ring development at the tree-ring scale.

To gain deeper insight into the respective roles of climatic variables on annual radial growth and WD, the radial growth of two Norway spruce trees was recorded daily over 4 years, with point dendrometers placed at four heights on each tree stem. Our objective was to determine to what extent short-term variations in climatic parameters influence growth and how wood density varies within a single growing season in response to these fluctuations. We hypothesized that climate

fluctuations are reflected in the annual wood density profile and not solely in latewood or maximum density.

Materials and methods

Study site

The study site, which supported an even-aged Norway spruce stand, is located near Nancy, northeastern France (48°44' N, 6°14' E, altitude 250 m a.s.l.). The soil is loamy and about 60 cm deep, with a soil water reserve estimated from soil texture of about 140 mm. The two dominant Norway spruce trees selected for the experiment were planted in 1970 on a flat area. At the beginning of the experiment in 1994, Tree 1 and Tree 2 were 15.9 and 15.3 m tall, with diameters at breast height of 18.3 and 18.5 cm, respectively, and 26 growth rings at breast height.

Growth monitoring

In summer 1994, both trees were equipped with electronic point-dendrometers fixed along the stem at heights of 0.25, 3, 9 and 12.5 m above ground for Tree 1, and at heights of 0.25, 3, 7 and 11.5 m for Tree 2. Dendrometers consisted of stainless-steel rods fixed to the trunk and a micrometric displacement transducer (LVDT Displacement Transducer, type DG5 Solartron, Solartron Metrology) positioned perpendicularly to the stem, 15 cm above the point of attachment. Changes in tree external radius were recorded every hour at a resolution of 3 μm . Radial measurements were recorded by a data logger (Campbell 21X, Campbell Scientific).

Meteorological data

Climatic data, which were collected at an automatic weather station about 500 m from the stand, included mean, minimum and maximum temperatures, vapor pressure deficit, solar radiation and precipitation. Daily estimates of the climatic data were used in our experiments. Potential evapotranspiration (PET, mm) was calculated according to the Penman (1948) formula. A simple water balance model was computed to estimate soil water reserves at daily time steps, and to quantify the soil water deficit. The model is given by:

$$R_n = R_{n-1} + (P - \text{Int})_n - T_n - D_n \quad (1)$$

where R_n is soil water reserve at day n ($R_n \leq R_{\text{max}}$), R_{max} is soil water reserve at field capacity, P is precipitation, Int is canopy interception, T is transpiration, and D is water loss, all at day n .

If

$$(R_{n-1} + (P - \text{Int})_n - T_n) > R_{\text{max}}, \quad (2)$$

then

$$D_n = R_{\text{max}} - (R_{n-1} + (P - \text{Int})_n - T_n) \quad (3)$$

Water stress is assumed to occur when soil water content drops below 40% of R_{max} (Granier et al. 1999). Based on this assumption, drought-induced reductions in transpiration were reproduced in the model. Transpiration was modeled as a function of PET and R_{n-1} as: $T/\text{PET} = 0.75$ when $R_{n-1} > 0.4R_{\text{max}}$, and $T/\text{PET} = (R_n - 1/R_{\text{max}})(0.75\text{PET})$ when $R_{n-1} < 0.4R_{\text{max}}$. Soil water deficit was calculated as $0.4R_{\text{max}} - R_n$ when $R_n < 0.4R_{\text{max}}$.

Dendrometer data analysis

Potentiometer data corresponding to radial positions in growth rings were converted to corresponding dates during the growing season. The time series of tree radii included periods of shrinkage and swelling that generate a non-monotonous relationship between time and position (Figure 1). Numerous studies have reported such hourly and daily changes in stem radius in Norway spruce (e.g., Zweifel et al. 2000, 2001, Offenthaler et al. 2001, Zweifel and Häslner 2001). These variations are closely linked to tree water status, because the course of xylem water potential is reflected in stem diameter fluctuations (Panterne et al. 1998, Downes et al. 1999, Offenthaler et al. 2001). To extract cambium growth information, we established the increment curves on the basis of the daily maximum values instead of mean values. The highest stem water potential values occurred at daily radius maximum values. Before the onset of growth, the tree radius value taken as the origin for the radial growth measurements was measured when the soil water reserve was fully recharged by winter rains (data not

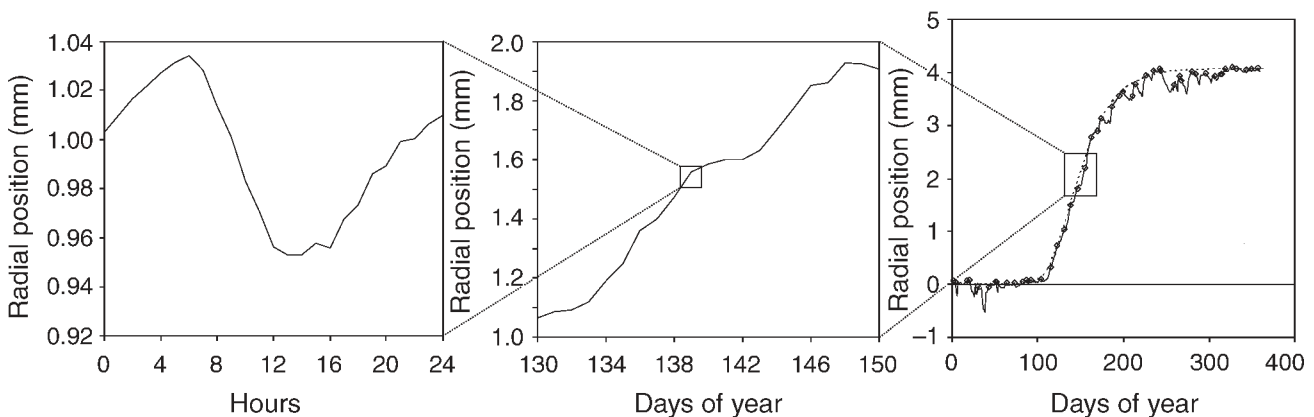


Figure 1. Hourly (left), daily (center) and yearly (right) time courses of changes in the radius of Tree 1 at a stem height of 12.5 m. The right-hand panel shows daily maximum radius (solid line) and the Gompertz function (dotted line) fitted to data (\diamond) for selected days.

shown).

In a second step, we selected the maximum tree radius over 7 days and fitted a Gompertz model to data selected to eliminate the effect of shrinkage on model fitting. Because this model is asymptotic, the cessation of growth was chosen when (Ring width day_n – Ring width day_{n-1}) is less than 0.003 mm (dendrometer measurement resolution). The resulting model was then used as a template to convert positions in rings to dates.

Analysis of intra-annual growth variations

Radial increment rates were determined by taking the radial distance from one daily maximum to the next over a 5-day time step (hereafter termed a pentad). The resulting chronological series showed large variations. The data were further transformed to remove medium- and low-frequency oscillations. In a first step, data were detrended by fitting a spline function (Figure 2A). Values of fitted splines were considered to represent medium-term oscillations. Residuals, referred to as short-term variations (Figure 2B), were further standardized by means of auto-regressive moving average (AR(p)MA(q)) models (Guiot 1986) selected according to the Akaike Information Criterion. In most cases, the simple model ARMA(1,0) was sufficient to reduce model residuals to white noise, but in years with larger growth fluctuations such as 1996

and 1998, models ARMA(1,1) or ARMA(2,1) fitted best. Four growth index chronologies were computed by averaging series from the two trees at each observation height (i.e., one per height). Climatic variables were standardized by specific spline functions to avoid fortuitous correlation with the pentad growth index series. The chronologies and all statistical analyses were performed with SAS software (Version 8.01, SAS Institute, Cary, NC).

Densitometric measurements

The two trees were felled after the 4 years of growth monitoring, and disks were cut where the dendrometers had been located. From each disk, radial samples following the point dendrometer axis were sawn for densitometric analyses. The samples were conditioned to a 12% water content and resawn in the transverse plane to a thickness of 2 mm. X-Ray negative photographs of the disks were obtained as described by Leban et al. (2004). The resulting X-ray picture was digitized and processed with CERD software (Mothe et al. 1998). The wood density profiles obtained are for each ring and are based on 100 measured positions.

Results

During the 4 years of growth monitoring, trees experienced greatly differing growth conditions. Potential evapotranspiration (PET) cumulated over the growing season (from April to September) varied from 643 to 718 mm, whereas precipitation varied from 290 to 410 mm. According to the water balance model, 1996 was a growth-constraining year with an early dry period, whereas 1995 was highly favorable for radial growth. Reflecting these differences in climatic conditions, there were large between-year differences in mean ring widths and densities (Table 1).

Growth monitoring

Radial growth started at the beginning of April, i.e., from days of the year (DOY) 90 to 110. No delay in the onset of growth was detected across trees at a given observation height, or among heights within a tree. Growth cessation occurred in August or September, with between-year differences of up to 1 month (DOY 230 to 260). The intra-annual pattern of growth comprised a period of accelerating growth in April (lasting almost 1 month, until DOY 120) followed by a long period when growth rate was constant, and a final period of slow growth (Figure 3). The duration of the period of rapid growth varied substantially from one year to another. During the rainy year 1995, rapid growth lasted until August (DOY 215), compared with mid-June (DOY 170) in 1996. The numerous decreases in radial growth rate, which occurred in 1996 and 1998, were closely related to the calculated soil water deficit (Figure 4). The decrease in growth rate observed in 1996 after mid-June corresponded to frequent soil water reserve deficits, which limited transpiration (i.e., soil water reserve dropped below 40%). The succession of rainy episodes (also in 1998) resulted in spike-like growth patterns, probably associated with changes in stem water potential. In 1998, a severe dry period stopped growth at the lowest observation points (0.25 and 3 m)

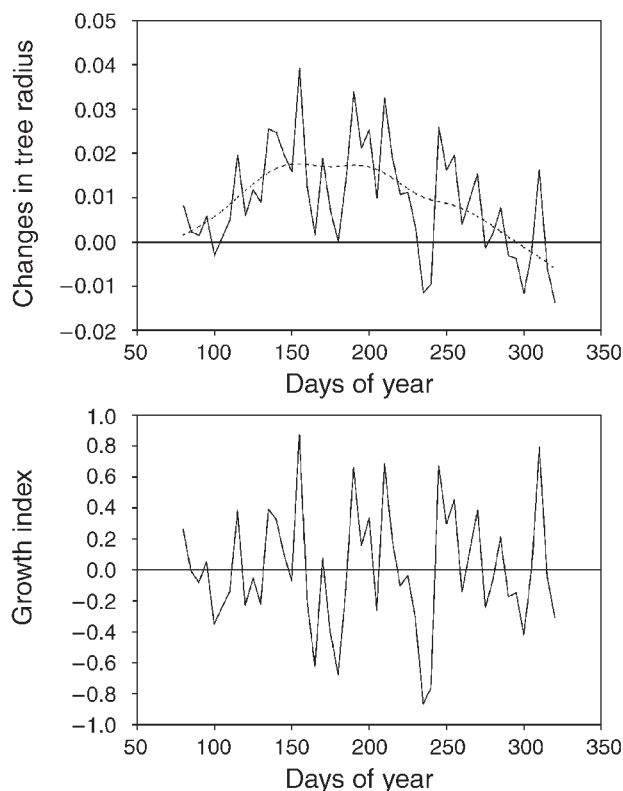


Figure 2. (A) Pentad changes in intra-annual tree radius. The solid line indicates short-term growth variations and the dashed line, which is the fitted spline function for Tree 1 (at 3 m height) in 1995, indicates medium-term growth variations. (B) Short-term growth variations as illustrated by the growth index resulting from spline detrending.

Table 1. Mean yearly characteristics of climate and rings studied. Abbreviations: CWD = cumulated water deficit; PET = cumulated potential evapotranspiration; RF = rainfall; and T_{mean} = mean temperature.

Year	T_{mean} (°C)	RF (mm)	PET (mm)	CWD	Ring characteristic	Stem height: Tree 1 (m)				Stem height: Tree 2 (m)			
						0.25	3	9	12.5	0.25	3	9	12.5
1995	14.9	411	643	579	Width (mm)	1.81	1.96	2.21	5.16	2.86	2.76	3.28	3.16
					Wood density (kg m^{-3})	471	542	466	406	354	492	387	416
1996	14.0	290	674	981	Width (mm)	1.49	1.35	2.45	3.91	1.64	1.69	2.07	2.04
					Wood density (kg m^{-3})	540	526	417	413	427	481	423	429
1997	15.1	394	718	842	Width (mm)	1.28	1.43	2.92	4.7	2.58	1.62	2.54	2.18
					Wood density (kg m^{-3})	466	515	401	395	376	490	408	419
1998	15.1	348	669	1580	Width (mm)	0.68	0.98	1.91	2.87	1.2	0.99	1.68	1.27
					Wood density (kg m^{-3})	487	513	400	500	400	503	397	420

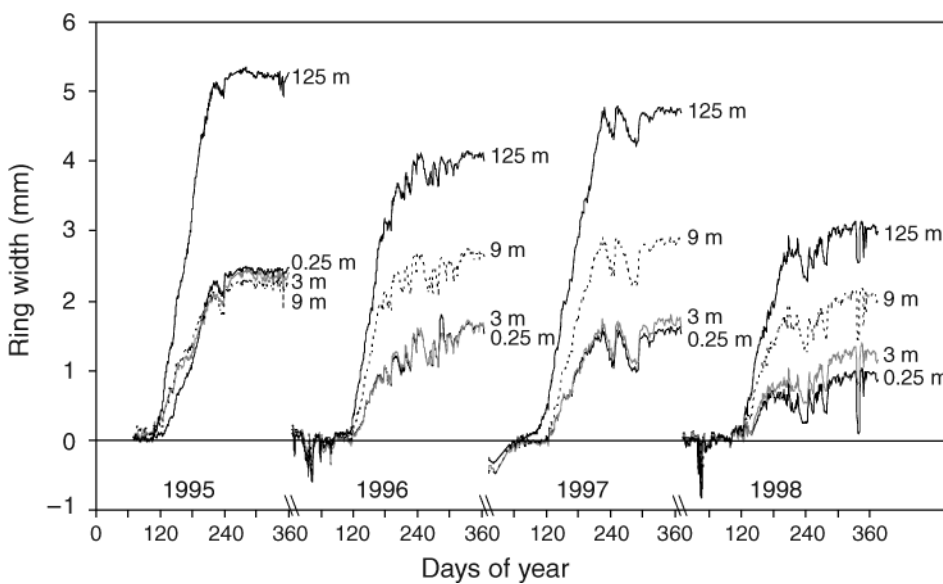


Figure 3. Intra-annual radial growth dynamics for Tree 1 at four stem heights during the years 1995–1998.

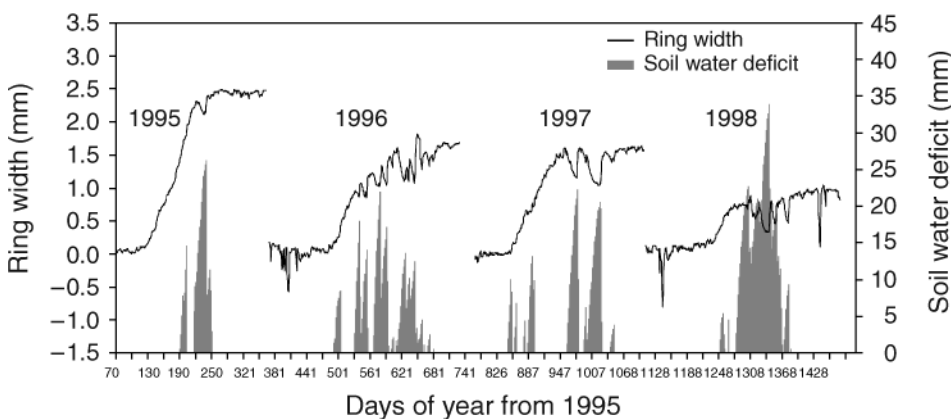


Figure 4. Comparison of intra-annual ring widths in Tree 1 (at a stem height of 3 m) and soil water deficits during the years 1995–1998.

in both trees, whereas growth was still observed higher up the stem. Overall, half of the annual radial growth was completed by the end of May, another third of annual growth was completed in June, and 95% was completed by the end of July. Ring segment formation took up to six times longer in late-

wood than in earlywood. The transition time between earlywood and latewood varied with annual climatic conditions. In the favorable years for radial growth (i.e., 1995 and 1997), the transition occurred in early August, compared with mid-June in the dry years.

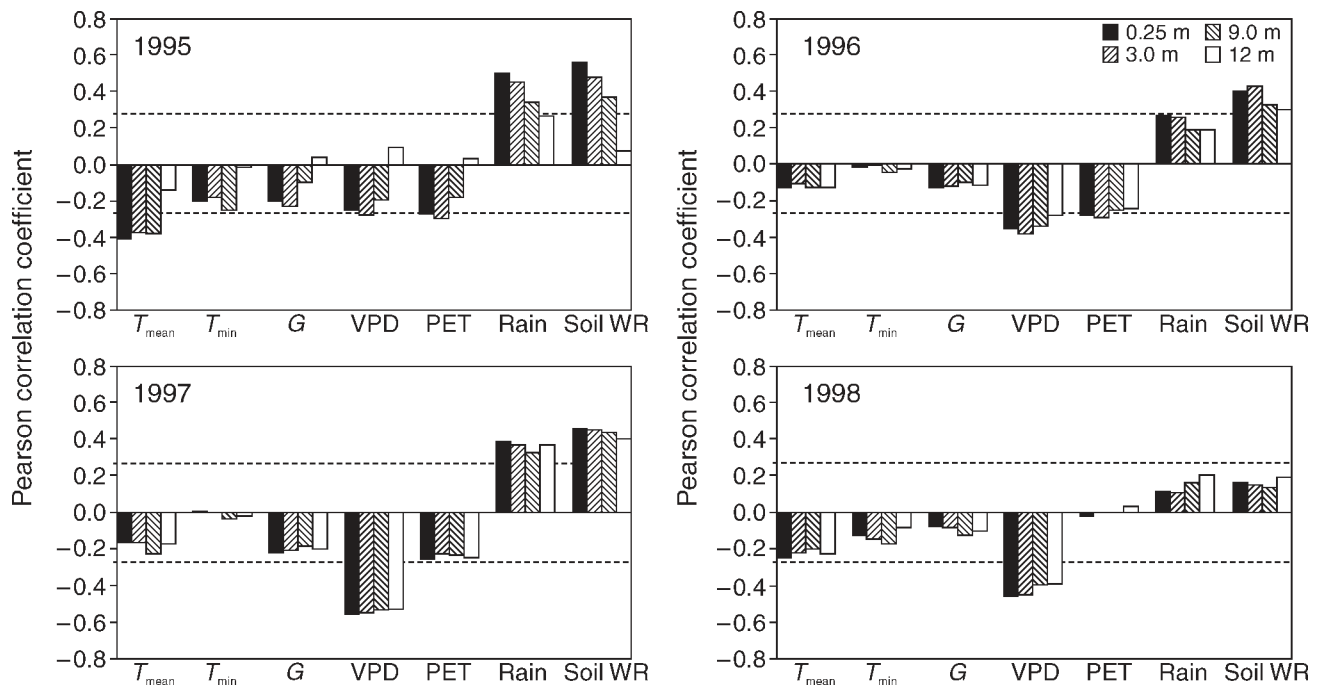


Figure 5. Correlations between standardized pentad increment variations and climatic characteristic at four stem heights (0.25, 3, 9 and 12.5 m; $n = 48$) in the years 1995–1998. Abbreviations: T_{mean} = mean day temperature; T_{min} = mean daily minimum temperature; G = daily radiant flux; VPD = vapor pressure deficit; PET = cumulated potential evapotranspiration; Rain = Rainfall cumulated precipitation; and Soil WR = mean soil water reserve. The dashed line denotes the significance threshold at $P < 0.05$.

Short-term growth variations

The standardized pentad variations in growth rate (Figure 2B) were correlated with climatic parameters. Mean daily temperature had a slightly negative effect on growth rate, which was significant only in 1995, except at a stem height of 12.5 m (Level 4) (Figure 5). Vapor pressure deficit had more marked effects on radial growth rate than temperature, and its effects were consistent from year to year. Pentad cumulated rainfall was the most important climatic variable affecting radial growth rate, with which it showed strong positive correlations, even when water availability was high, as in 1995 and 1997. Soil water reserves estimated with the simplified water balance model gave higher correlations with radial growth rate than rainfall, underlying the key role of water supply in radial growth. In 1996 and 1997, the correlations between basic climate characteristics and radial growth may have been affected by the drought events that reduced growth rates (Figure 6).

Correlations between radial growth and climate indicated differences in sensitivity depending on the height on the stem at which growth was monitored. Pentad cumulated rainfall, mean VPD and soil water reserve gave the best correlations with radial growth at the stem base. Multiple regression models confirmed this pattern and showed that climate characteristics explained radial growth variations at the two lowest observation points best (Table 2). Moreover, the best model according to Mallows's $C(p)$ did not have the same independent variables. It appears that ring growth is less sensitive to soil water reserves in the upper than in the lower part of the stem.

Density profiles

Intra-ring wood density variations are plotted against DOY for the years 1995–1998 in Figure 7. The difference between the maximum and minimum local density, known as density contrast, reached 800 kg m^{-3} for one particular ring. The density profiles showed a synchronic density peak (false ring) in 1996. The superposition of the density profile with the dynamics of estimated drought severity revealed that the false ring corresponds to a dry period (Figure 8). Figure 8 shows that a period of higher water deficit that occurred in 1997 corresponded to a slight increase in density in the earlywood part of the ring, which confirms the high sensitivity of wood density to water deficit. The patterns of increasing density from earlywood to latewood were correlated with temperature, radiation and VPD, all of which increase from the early to the late part of the growing season.

Examination of the 1996 ring (Figure 8) indicates that the period of water deficit induced a local reduction in cell size, which corresponds with a decline in radial growth rate. Hence we hypothesized that variations in wood density are linked with medium-term variations in growth rate. If true, this would imply a trade-off between growth rate and wood density. Medium-frequency growth variations were estimated using the spline function. Wood density showed a bimodal pattern of variation when plotted against growth rate (Figure 9). An initial period when variations in growth rate were not reflected by variations in wood density was followed by a period when variations in wood density and radial growth correlated closely. The pattern was found each year, with slight differ-

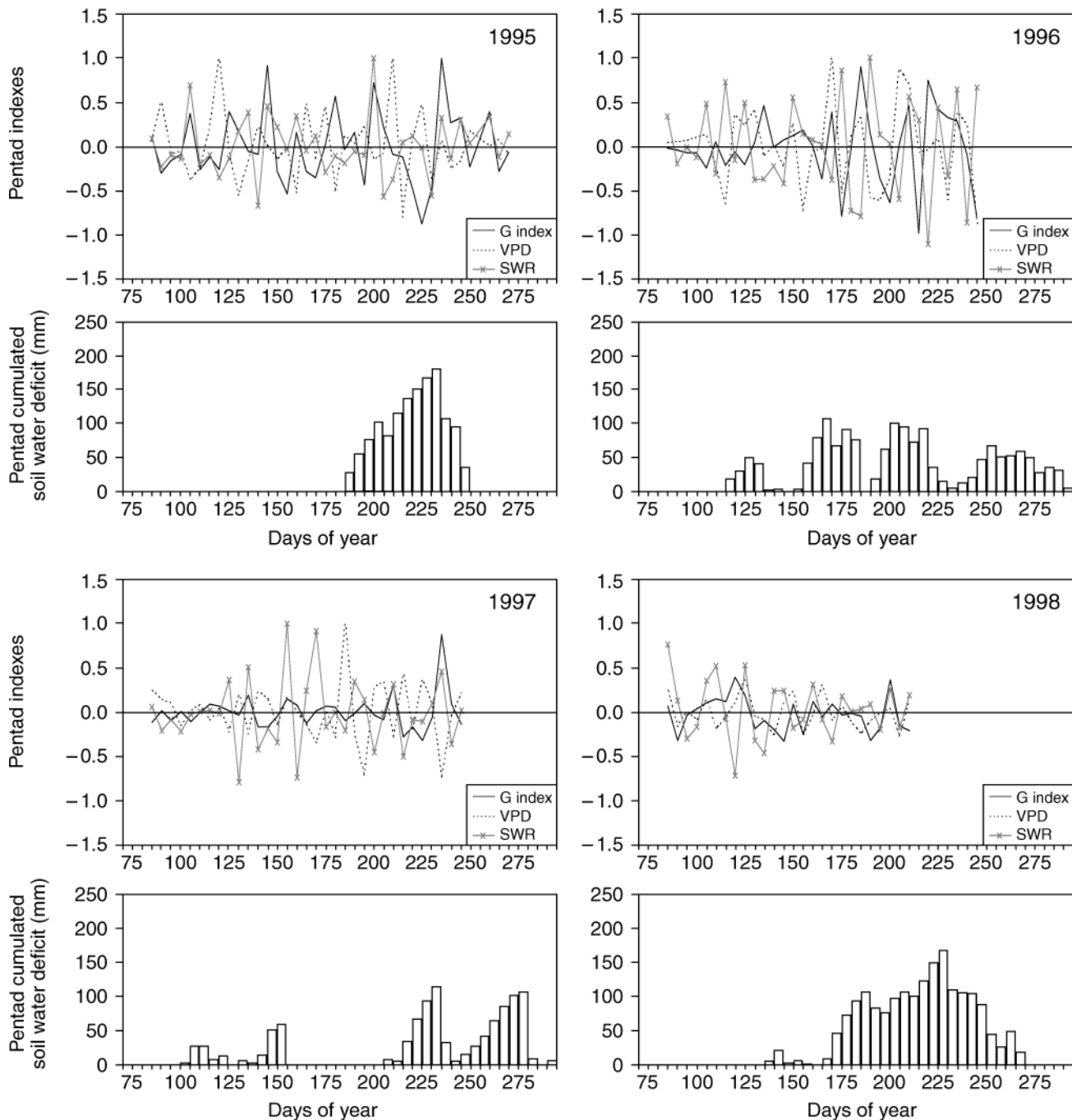


Figure 6. Seasonal variations in the stem radial growth index (G index) at a height of 3 m, vapor pressure deficit (VPD), soil water reserve status (SWR) and the parallel time course of soil water deficit.

ences in the slope of the relationship. The date of transition between the two periods was almost constant between years, occurring by the end of May in 1995, 1996 and 1997 and the transition occurred only 10 days earlier in 1998. At the time of the transition, half of the annual radial growth was already realized. The results displayed in Figure 9 suggest a new physiological definition for the transition between earlywood and latewood formation based on the date at which radial growth

rate peaks and wood density starts to increase.

Discussion

Radial growth and climate

We found that soil water deficit had large effects on radial growth at the intra-annual time scale. The trees studied were growing on a shallow soil but which, nevertheless, had a substantial water reserve. Precipitation and estimated soil water

Table 2. Results of multiple regression analyses of interannual pentad radial growth indices for the years 1995–1998 in two Norway spruce trees versus the independent variables: Rain = pentad rainfall (mm); SWR = pentad cumulated soil water deficit (mm); T_{mean} = mean pentad daily temperature ($^{\circ}\text{C}$); and WD = wood density. Time series started at day of year 90 and were stopped at the first pentad after cessation of tree growth, leading to unequal data length between years.

Year	Height along stem	Independent variables			n	Adj. R^2	Mallows C(p)
1995	0.25	Rain	SWR	T_{mean}	40	0.369	3.103
	3.0	Rain	SWR	T_{mean}	40	0.279	2.672
	9.0	Rain	T_{mean}		40	0.187	1.585
		Rain	SWR	T_{mean}	40	0.186	2.646
		Rain	VPD		40	0.079	2.985
		Rain	SWR	T_{mean}	40	0.054	5.189
1996	0.25	SWR	VPD	WD	38	0.286	2.197
	3.0	SWR	VPD	WD	38	0.341	2.045
	9.0	SWR	VPD	WD	38	0.246	2.045
	12.5	VPD	WD		38	0.178	1.755
		SWR	VPD	WD	38	0.189	2.166
1997	0.25	SWR	VPD	WD	38	0.353	2.488
	3.0	SWR	VPD	WD	38	0.354	2.291
	9.0	SWR	VPD	WD	38	0.347	2.070
	12.5	Rain	VPD	WD	38	0.363	2.440
		SWR	VPD	WD	38	0.279	8.291
	1998	0.25	VPD			36	0.192
3.0		VPD			36	0.188	0.261
9.0		VPD			36	0.136	0.288
12.5		VPD			36	0.132	0.396

reserve had significant effects on radial growth even during years with high rainfall. These results are in agreement with inter-annual studies in Norway spruce showing that radial growth is positively correlated with June precipitation in particular and with summer precipitation of the current year in general (Mäkinen et al. 2000, 2001). Soil water content is known to be a key parameter for determining tracheid size through its effect on turgor pressure control (Ryan et al. 1994). However, the reason for the link between precipitation and cell enlargement, and consequently radial growth, is not obvious. Stem water status is closely related to soil water reserve, which depends more on water balance than on water supply.

The effect of climate variation on radial growth was greater toward the stem base than higher up and were mediated by changes in soil water content. Similar observations in another dendrochronological study with spruce (Cherubini et al. 1996) support the idea that drought reduces photosynthate transportation, thereby limiting growth most severely at the stem base (Sevanto et al. 2003).

Wood density and climate

Unlike radial growth rate, wood density was influenced by climatic fluctuations only during the second half of the growing season. The wood density profiles of those portions of rings formed in the second half of the growing season were affected by drought. The strong positive correlation between soil water deficit and wood density can be attributed to a reduction in tracheid enlargement and an associated increase in the proportion of the various ring segments made up of cell walls. Soil

water potential and soil water content were greatly reduced during drought episodes, as illustrated by the reduction in stem radius (cf. Herzog et al. 1995, Mäkinen et al. 2003). Similarly, Abe and Nakai (1999) irrigated *Cryptomeria japonica* (D. Don.) trees every day or every three days and observed a significant difference in tracheid diameter between treatments.

In 1996, the drought effect was sufficient to generate false-ring (latewood-like cells in the earlywood) formation. Rozenberg et al. (2002) previously showed that water deficit can induce a false-ring during earlywood formation in Norway spruce and similar effects of drought have been observed in *Quercus ilex* L. (Zhang and Romane 1991). Based on a literature review, Cherubini et al. (2003) concluded that many woody species growing in the Mediterranean zone exhibit false rings. It is well known that soil water depletion promotes latewood initiation in several coniferous species including red pine (*Pinus resinosa* Ait.) (Zahner and Whitmore 1960), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) (Brix 1972) and loblolly pine (*Pinus taeda* L.) (Cregg et al. 1988). This behavior may be associated with drought tolerance in trees because, according to recent findings, latewood tracheids of spruce can tolerate extreme decreases in water potential while maintaining minimal conductivity (Mayr and Cochard 2003, Wimmer and Downes 2003).

Relationship between wood density and radial growth

We found that, during the first part of the growing season, climatic variations affected growth rate but not wood density. During the second part of the growing season, climatic varia-

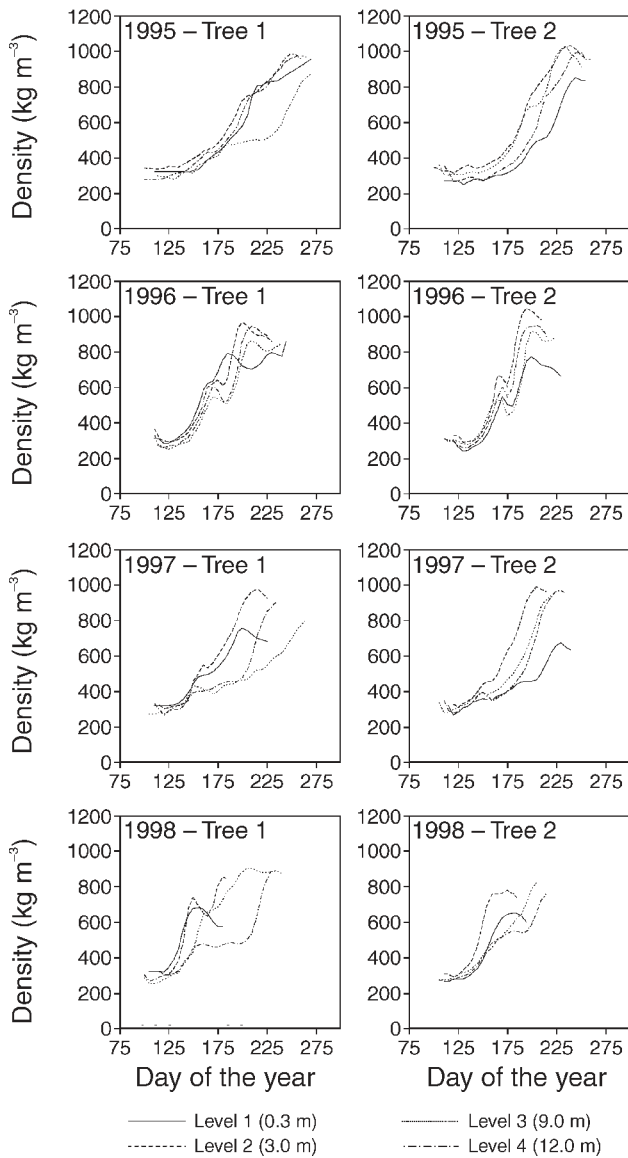


Figure 7. Intra-annual fluctuations in wood density (equivalent to wood density profiles) for two Norway spruce trees measured at four stem heights for the years 1995–1998.

tions reduced radial growth rate, resulting in increased wood density (Figure 9). Based on these findings, we suggest that the positive effect of temperature on wood density (Kienast et al. 1987, D'Arrigo et al. 1992, Yasue et al. 2000) is a consequence of its negative effects on radial growth rate. Similarly, the large effect of soil water depletion and water regime on wood density are consistent with their negative effects on radial growth.

Almost all of the relationships between climatic variables and wood density reported in the literature are based on maximum density of latewood only. The strength of the relationships between latewood density and climate can be explained on the basis of the duration of tracheid formation, which permits the integration of variation in climatic characteristics (Sass and Eckstein 1995, Schweingruber and Briffa 1996, Gindl et al. 2000). The existence of such a relationship is sup-

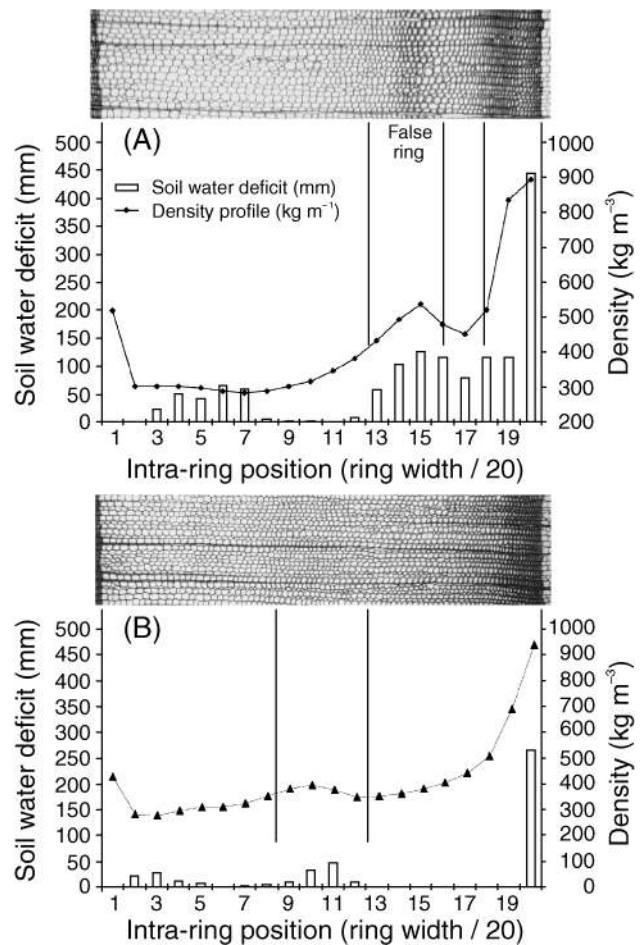


Figure 8. (A) A representative example of a ring density profile obtained in 1996 and the corresponding soil water deficit computed for each segment (of Tree 1, at a height of 12.5 cm (level 4)). (B) The 1997 growth ring of the same tree.

ported indirectly by data obtained in previous studies on intra-annual xylem development showing that the increased thickness of latewood tracheids results from an increase in the duration of wall material deposition, and not an increase in deposition rate (Whitmore and Zahner 1966, Wodzicki 1971). More recently, Horacek et al. (1999) reported a strong correlation between tracheid wall thickness and the duration of tracheid maturation in Norway spruce. They found a continuous and quasi steady-state rate of wall formation within both growth and differentiation zones. Based on these observations, we deduce that an increase in radial growth rate would decrease wall thickness proportionally.

The link that we found between radial growth pattern and variations in wood density during the second half of the growing season explains why latewood density variations are highly sensitive to climatic fluctuations, because radial growth rate is strongly influenced by climate, even at short time steps. In contrast, the lack of a relationship in the early parts of growth rings points to cambium control of earlywood radial growth rate. Stability in wood density during the first part of

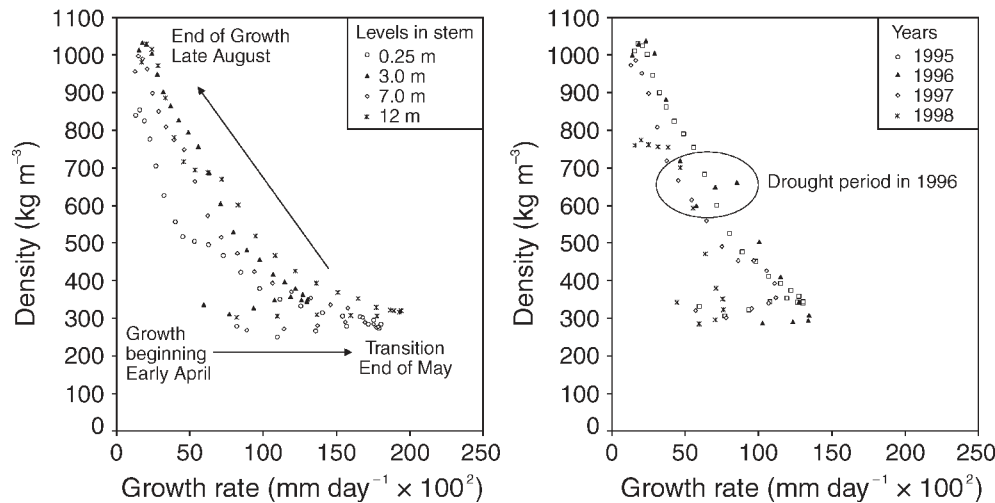


Figure 9. Pentad wood density as a function of growth rate in Tree 1: left, results for Tree 1 at every observation height in 1995; right, at a stem height of 3 m (level 2) for the years 1995–1998.

the growing seasons indicates that early wood radial growth rate, and hence density, was more or less constant even during the drought in early 1996 (Figure 8).

We conclude that dendrometers are a valuable tool for determining stem growth sensitivity to external factors, and for analyzing intra-annual variations in wood density. Because short-term variations in wood density are small, studying their relationship with pentad (and probably also weekly) growth rate fluctuations is probably not feasible. However, dendrometers offer sufficient precision to investigate annual patterns of radial growth and provide a basis for converting radial positions within a growth ring to a seasonal time scale. Dendrometers could play an important role in studies of the seasonal activity of the vascular cambium, because they allow measurement of long time series, without creating the disturbances associated with the pinning technique (Schmitt et al. 2000). The relationship between radial growth pattern and wood density profile requires further investigation on more trees and species and for different growing conditions and tree ages. If the robustness of the relationship found in this study holds across trees, species and environmental conditions, it will be particularly useful in the modeling of wood development.

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References

Abe, H. and T. Nakai. 1999. Effect of the water status within a tree on tracheid morphogenesis in *Cryptomeria japonica* D. Don. *Trees* 14:124–129.

- Becker, M., D. Bert, J. Bouchon, J.-L. Dupouey, J.-F. Picard and E. Ulrich. 1995. Long-term changes in forest productivity in north-eastern France: the dendroecological approach. *In* *Forest Decline and Atmospheric Deposition Effects in the French Mountains*. Eds. G. Landmann and M. Bonneau. Springer-Verlag, Berlin, pp 143–156.
- Briffa, K.R., P.D. Jones, F.H. Schweingruber, S.G. Shiyatov and E.R. Cook. 1995. Unusual twentieth-century summer warmth in a 1000-year temperature record from Siberia. *Nature* 376:156–159.
- Briffa, K.R., P.D. Jones, F.H. Schweingruber and T.J. Osborn. 1998. Influence of volcanic eruptions on Northern hemisphere summer temperatures over the past 600 years. *Nature* 393:450–455.
- Brix, H. 1972. Nitrogen fertilization and water effects on photosynthesis and earlywood–latewood production in Douglas fir. *Can. J. For. Res.* 2:467–478.
- Cherubini, P., P. Piussi and F.H. Schweingruber. 1996. Spatiotemporal growth dynamics and disturbances in a subalpine spruce forest in the Alps: a dendrochronological reconstitution. *Can. J. For. Res.* 26:991–1001.
- Cherubini, P., B. Gartner, R. Tognetti, O.U. Bräker, W. Schoch and J.L. Innes. 2003. Identification, measurement and interpretation of tree rings in woody species from Mediterranean climates. *Biol. Rev.* 78:119–148.
- Cregg, B.M., P.M. Dougherty and T.C. Hennessey. 1988. Growth and wood quality of young loblolly pine trees in relation to stand density and climatic factors. *Can. J. For. Res.* 18:851–858.
- Cubash, U., J. Waszkewitz, G. Hegerl and J. Perlwitz. 1995. Regional climate changes as simulated in time-slice experiments. *Climate Change* 31:273–304.
- D’Arrigo, R.D., G.C. Jacoby and R.M. Free. 1992. Tree ring width and maximum latewood density at the North American tree line: parameters of climate change. *Can. J. For. Res.* 22:1290–1296.
- Decoux, V., E. Varcin and J.-M. Leban. 2004. Relationships between the intra-ring wood density assessed by X-ray densitometry and optical anatomical measurements in conifers. Consequences for the cell wall apparent density determination. *Ann. Sci. For.* 61: 251–262.
- Deleuze, C. and F. Houllier. 1998. A simple process-based xylem growth model for describing wood microdensitometric profiles. *J. Theor. Biol.* 193:99–113.
- Downes, G., C. Beadle and D. Worledge. 1999. Daily stem growth pattern in irrigated *Eucalyptus globulus* and *E. nitens* in relation to climate. *Trees* 14:102–111.

- Gindl, W., M. Grabner and R. Wimmer. 2000. The influence of temperature on lignin content in treeline Norway spruce compared with maximum density and ring width. *Trees* 14:409–414.
- Granier, A., N. Bréda, S. Biron and S. Villette. 1999. A lumped water balance model to evaluate duration and intensity of drought constraints in forest stands. *Ecol. Model.* 116:269–283.
- Guiot, J. 1986. ARMA techniques for modelling tree-ring response to climate and for reconstructing variations of paleoclimates. *Ecol. Model.* 33:149–171.
- Herzog, K.M., R. Häsler and R. Thum. 1995. Diurnal changes in the radius of a subalpine Norway spruce stem: their relation to the sap flow and their use to estimate transpiration. *Trees* 10:94–101.
- Horacek, P., J. Slezingerova and L. Gandelova. 1999. Effects of environment on the xylogenesis of Norway spruce (*Picea abies* [L.] Karst.). In *Tree-ring Analysis: Biological, Methodological and Environmental Aspects*. Eds. R. Wimmer and R.E. Vetter. CABI Publishing, CAB International, Wallingford, Oxon., pp 33–54.
- Hughes, M.K., F.H. Schweingruber, D. Cartwright and P.M. Kelly. 1984. July–August temperature at Edinburgh between 1721 and 1975 from tree-ring density and width data. *Nature* 308:341–344.
- IPCC. 2001. Climate change 2001: the scientific basis. In *Contribution of Working Group I to the Third Assessment Report of the IPCC*. Cambridge University Press, Cambridge, 83 p.
- Kienast, F., F.H. Schweingruber, O.U. Bräker and E. Schär. 1987. Tree-ring studies along ecological gradients and the potential of single-year analyses. *Can. J. For. Res.* 17:683–696.
- Leban, J.-M., A. Pizzi, S. Wieland, M. Zanetti, M. Properzi and E. Pichelin. 2004. X-Ray microdensitometry analysis of vibration-welded wood. *J. Adhes. Sci. Technol.* 18:673–685.
- Mäkinen, H., P. Nöjd and K. Mielikäinen. 2000. Climatic signal in annual growth variation of Norway spruce (*Picea abies*) along a transect from central Finland to the Arctic timberline. *Can. J. For. Res.* 30:769–777.
- Mäkinen, H., P. Nöjd and K. Mielikäinen. 2001. Climatic signal in annual growth variation of Norway spruce (*Picea abies*) in southern Finland. *Trees* 15:177–185.
- Mäkinen, H., P. Nöjd and P. Saranpää. 2003. Seasonal changes in stem radius production of new tracheids in Norway spruce. *Tree Physiol.* 23:959–968.
- Mayr, S. and H. Cochard. 2003. A new method for vulnerability analysis of small xylem areas reveals that compression wood of Norway spruce has lower hydraulic safety than opposite wood. *Plant Cell Environ.* 26:1365–1371.
- Mothe, F., G. Duchanois, J.-M. Leban and G. Nepveu. 1998. Analyse microdensitométrique appliquée au bois: une méthode de traitement des données aboutissant à la description synthétique et homogène des profils de cerne (programme CERD). *Ann. For. Sci.* 55:301–315.
- Offenthaler, I., P. Hietz and H. Richter. 2001. Wood diameter indicates diurnal and long-term patterns of xylem water potential in Norway spruce. *Trees* 15:215–221.
- Panterne, P., J. Burger and P. Cruziat. 1998. A model of the variation of water potential and diameter within a woody axis cross section under transpiration conditions. *Trees* 12:293–301.
- Parker, M.L. and W.N.S. Hensch. 1971. The use of Engelmann spruce latewood density for dendrochronological purposes. *Can. J. For. Res.* 1:90–98.
- Penman, H.L. 1948. Natural evaporation from open water, bare soils and grass. *Proc. R. Soc. A* 193:120–145.
- Rozenberg, P., J. Van Loo, B. Hannrup and M. Grabner. 2002. Clonal variation of wood density record of cambium reaction to water deficit in *Picea abies* (L.) Karst. *Ann. Sci. For.* 59:533–540.
- Ryan, D.A.J., D.L. McLaughlin and A.M. Gordon. 1994. Interpretation of sugar maple (*Acer saccharum*) ring chronologies from central and southern Ontario using a mixed linear model. *Can. J. For. Res.* 24:568–575.
- Sass, U. and D. Eckstein. 1995. The variability of vessel size in beech (*Fagus sylvatica* L.) and its ecophysiological interpretation. *Trees* 9:247–252.
- Schmitt, U., R. Möller and D. Eckstein. 2000. Seasonal wood formation dynamics of beech (*Fagus sylvatica* L.) and black locust (*Robinia pseudoacacia* L.) as determined by the “pinning” technique. *J. Appl. Bot.* 74:10–16.
- Schweingruber, F.H. and K.R. Briffa. 1996. Tree-ring density for climate reconstruction. In *Climatic Variations and Forcing Mechanisms of the Last 2000 Years*. Eds. P.D. Jones, S.B. Raymond and J. Jouzel. Springer-Verlag, Berlin, pp 43–66.
- Schweingruber, F.H., H.C. Fritts, O.U. Bräker, L.G. Drew and E. Schär. 1978. The X-ray technique as applied to dendroclimatology. *Tree Ring Bull.* 38:61–91.
- Sevanto, S., T. Vesala, M. Perämäki and E. Nikinmaa. 2003. Sugar transport together with environmental conditions controls time lags between xylem and stem diameter changes. *Plant Cell Environ.* 26:1257–1265.
- Spiecker, H., K. Mielikäinen, M. Köhl and J.P. Skovsgaard. 1996. Growth trends in European forests. Springer-Verlag, Berlin, 372 p.
- Whitmore, F.W. and R. Zahner. 1966. Development of the xylem ring in stems of young red pine trees. *For. Sci.* 12:198–210.
- Wimmer, R. and G.M. Downes. 2003. Temporal variations of the ring width–wood density relationship in Norway spruce grown under two levels of anthropogenic disturbance. *IAWA J.* 24:53–61.
- Wodzicki, T.J. 1971. Mechanism of xylem differentiation in *Pinus sylvestris* L. *J. Exp. Bot.* 22:670–687.
- Yasue, K., R. Funada, O. Kobayashi and J. Ohtani. 2000. The effect of tracheid dimensions on variations in maximum density of *Picea glehnii* and relationships to climate factors. *Trees* 14:223–229.
- Zahner, R. and F. Whitmore. 1960. Early growth of radically thinned loblolly pine. *J. For.* 58:628–634.
- Zhang, S.H. and F. Romane. 1991. Variations de la croissance radiale de *Quercus ilex* L. en fonction du climat. *Ann. Sci. For.* 48:225–234.
- Zweifel, R. and R. Häsler. 2001. Dynamics of water storage in mature subalpine *Picea abies*: temporal and spatial patterns of change in stem radius. *Tree Physiol.* 21:561–569.
- Zweifel, R., H. Item and R. Häsler. 2000. Stem radius changes and their relation to stored water in stems of young Norway spruce trees. *Trees* 15:50–57.
- Zweifel, R., H. Item and R. Häsler. 2001. Link between diurnal stem radius changes and tree water relations. *Tree Physiol.* 21:869–877.