Using simple causal modeling to understand how water and temperature affect daily stem radial variation in trees

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Summary Variation in tree stem diameter results from reversible shrinking and swelling and irreversible radial growth, all processes that are influenced by tree water status. To assess the causal effects of water and temperature on stem radial variation (ΔR) and maximum daily shrinkage (MDS), the diurnal cycle was divided into three phases: contraction, expansion and stem radius increment. Diurnal cycles were measured during 1996–2004 in Picea abies (L.) Karst., Pinus cembra L. and Larix decidua Mill. in a timberline ecotone to understand the links between stem diameter variation (v; defined as MDS or ΔR), phase duration (h), and weather or sap flow descriptors (d). We demonstrated that a high proportion of MDS and ΔR was explained by h because of the nonlinearity of the physiological responses to weather d. By causal modeling, we tested whether the relationship between d and v was due to h (lack of causal relationship between d and v) or to both d and h (double cause). The results of this modeling added new physiological insight into daily growth–climate relationships. Negative correlations were found between ΔR and air temperature owing to the negative effect of temperature on h only, and did not correspond to a direct effect on tree growth mediated by an alteration in metabolic activities. Precipitation had two main effects: a direct effect on ΔR and an indirect effect mediated through an effect on h. A reduction in sap flow at night led to an increase in ΔR for P. abies and L. decidua, but not for P. cembra.

Keywords: conifers, growth–climate relationships, radial growth, stem contraction, tree-water relations.

Introduction

Daily stem diameter variations in trees result from depletion and replenishment of stem water stored in tissues and radial growth (Kozlowski and Winget 1964, Herzog et al. 1995, Irvine and Grace 1997, Génard et al. 2001, Daudet et al. 2005, Steppe et al. 2006). Several studies have been undertaken to link stem radial variations with climate (Downes et al. 1999, Tardif et al. 2001, Deslauriers et al. 2003, Mäkinen et al. 2003, Bouriaud et al. 2005, Zweifel et al. 2006), but interpretation of the results is uncertain because of the superimposed effects of both water status and cambial activity.

During tree growth, xylem and phloem elements are produced by way of cell division, extension of primary cell walls, secondary wall formation and lignification, all processes regulated by gene expression (Schrader et al. 2004), hormonal signals (Schrader et al. 2003) and environmental factors (Savidge 1996, Deslauriers and Morin 2005, Rossi et al. 2006). Cellular enlargement is basically water-dependent, because turgor pressure drives irreversible cell expansion and deposition of wall polymers (Proseus and Boyer 2005). Consequently, the two main processes measured by dendrometers, reversible diameter changes and radial growth, are both water-dependent. Mathematical models and experimental data support the concept that daily increases in stem diameter are caused by replenishment of water in storage tissues and stem growth (Steppe et al. 2006) and that the current tree water status plays a greater role in stem diameter variation than the carbon (C) balance (Daudet al. 2005, Zweifel et al. 2006).

Consideration of the large effects of tree water status on cell division and enlargement (Abe et al. 2003, Proseus and Boyer 2005) provides an explanation of the effects of water on stem diameter variation measured by dendrometers. A positive influence of water on radial stem growth has been observed for a wide range of species, including Eucalyptus spp. (Downes et al. 1999), Pinus hartwegii Lindl. (Biondi et al. 2005), Abies balsamea (L.) Mill. (Deslauriers et al. 2003), Picea abies (L.) Karst. (Bouriaud et al. 2005, Zweifel et al. 2006), Quercus pubescens Willd. and Pinus sylvestris L. (Zweifel et al. 2006). Less well understood effects include the negative relationship between temperature and growth rate in P. abies in France (Bouriaud et al. 2005) and in several boreal conifer species (Tardif et al. 2001). Temperature is a primary determinant of growth and has been found to influence cell production in several European conifer species (Antonova and Stasova 1997, Rossi 2003). However, the question remains as to how closely the relationship is directly causal. It is thus of interest to distinguish unambiguously the causal effects of tissue water status and temperature on stem radial variation to better interpret growth–climate relationships.

The stem cycle approach introduced by Downes et al.
(1999) might be a tool for better understanding the effects of different factors on stem radial variations. It divides the typical stem circadian cycle into three phases: contraction, recovery and stem radius increment (i.e., estimated radial growth). By following periodic sap flow variations, the stem cycle approach provides an accurate assessment of both components of the stem cycle: phase duration and stem radial variation (\(v\)), which is defined as stem radius variation (\(\Delta R\)) and maximum daily shrinkage (MDS). To date, the components of the stem cycle have been analyzed separately but the effect of climate on duration has been ignored. Downes et al. (1999) assumed these components were physiologically independent. However, phase duration could be highly dependent on climate variation, because stem shrinking and swelling are driven by tree transpiration and sap flow (Herzog et al. 1995, Perämäki et al. 2001).

In this study, two components of the stem circadian cycle, duration of the different phases (\(h\)) and the corresponding \(v\) (MDS or \(\Delta R\)) were analyzed on a daily basis to assess their relationships with water status and temperature. The hypotheses of causal relationships between descriptors (weather and sap flow variables), \(h\) and \(v\) (MDS or \(\Delta R\)) were tested by two models in which the correlation between descriptor and \(v\) is caused by \(h\) only, or by both descriptor and \(h\). Both models are based on two initial hypotheses: correlation between (1) descriptors and \(h\); and (2) \(h\) and \(v\). This approach should allow us to better explain the effect of temperature on \(v\), which is particularly important in high-altitude forests. To verify the models, the dynamics of \(v\) were recorded for 9 years with automatic band dendrometers on individuals of the three main conifer species at the Italian Alpine timberline.

Material and methods

Study area

The study was conducted in the northeastern Italian Alps (Dolomites, Cortina d’Ampezzo (BL), 46°27′ N 12°08′ E). The site is at 2080 m a.s.l. near the Cinque Torri mountain group on a south facing slope of about 30%, within a mixed open forest with groups of 5–15 trees of larch (\(Larix decidua\) Mill.) and stone pine (\(Pinus cembra\) L.) and the occasional Norway spruce (\(Picea abies\) (L.) Karst.), corresponding to the timberline ecotone definition (Körner 1998). The timberline originated from abandoned pasture lands with tree establishment occurring from 1943 to 1971. The climate at the site is typical of the southeastern Alps. The winters are dry with most precipitation occurring during summer and early autumn. Two trees each of \(P.\ abies\) (91 ± 11.3 cm diameter at breast height (dbh), 10.4 ± 0.6 m height, 45.0 ± 8.7 years old), \(L.\ decidua\) (79 ± 1.2 cm dbh, 11.6 ± 1.0 m height, 60.6 ± 18.7 years old) and \(P.\ cembra\) (103 ± 14.1 cm dbh, 10.1 ± 0.7 m height, 60.4 ± 7.9 years old) were monitored from 1996 to 2004.

Data collection

Stem radius variation, climate and sap flow were monitored from 1996 to 2004 and recorded with data loggers. Automatic band dendrometers (Tecno Penta, Teolo (PD), Italy) were used to monitor \(v\) continuously. These instruments measure linear displacement of a stainless-steel band wrapped around the trunk. The operating principle is based on the use of a linear potentiometer. Displacement is resolved to 6 µm over an unadjusted range of 20 mm. As the stem expands and contracts, the band transmits a signal to the potentiometer. The band had a thermal coefficient of linear expansion of 11 µm m\(^{-1}\) °C\(^{-1}\), representing an error of about 1% on the calculated values of MDS and \(\Delta R\). Teflon foils were placed between bark and band to reduce friction. Dendrometers were installed on two trees per species at a height of about 1.3 m. Readings were taken every 15 minutes and the hourly means calculated. To obtain radial measurements, the circumference data were divided by 2\(\pi\).

A 2-m-tall weather station was installed in an open area in the middle of the site. Air temperature (°C) and relative humidity (%) at a height of 2 m were measured each minute and recorded as 15-min means. Other variables were measured each minute and stored every hour. Soil water content (%) was measured with a time domain reflectometer (TDR method) at 15–20-cm depth. The rainfall sum (mm) was recorded each hour from the 1-min measurements. Vapor pressure deficit (VPD, kPa) was calculated from the hourly means of air temperature and relative humidity (Jones 1992). Sap flow density (dm\(^3\) dm\(^{-2}\) h\(^{-1}\)) was measured in each tree with a continuously heated thermal dissipation sensor (2-cm-long needle) (Granier 1985). The sensors were inserted in the xylem at about 1.5 m aboveground, on the northwest side of the stem. Protection from high solar radiation was ensured by insulating shields placed over the sensors and, for \(P.\ abies\) and \(P.\ cembra\), by the dense tree branches reaching the ground. Measurements were taken each minute and stored as 15-min means.

Extraction of stem variation and association with climate

For each tree and year, the stem cycle was divided into three distinct phases (Downes et al. 1999, Deslauriers et al. 2003): (1) a contraction phase, the period between the morning stem radius maximum and the afternoon minimum; (2) an expansion phase, the total period from the stem radius minimum to the next morning’s maximum; and (3) a stem radius increment phase, part of the expansion phase from the time when the stem radius exceeds the morning maximum until the subsequent maximum (Figure 1). The definition of the expansion phase is slightly different from that of Downes et al. (1999) (recovery phase) because we considered the whole expansion process (recovery and stem increment) (cf. Deslauriers et al. 2003). The difference between the expansion maximum and the onset of the stem radius increment phase represents the positive stem radius change estimate (\(\Delta R^+\), µm). When the previous cycle maximum was not reached, a negative stem radius change (\(\Delta R^-\), µm) was calculated but no increment phase was defined (Figure 1). Maximum daily shrinkage (µm) was calculated as the difference between the morning maximum and the afternoon minimum. The duration (\(h\), hours) of each phase was calculated. Any additional small effect of tempera-
ture on wood expansion did not affect the cycle amplitude and was ignored in the analysis. Similarly, variations caused by dead bark included in the dendrometer signal could not be removed. However, trees of the same species were of the same age and had bark that was of similar thickness.

From May to September, the stem cycle generally lasted about 24 h, but heavy precipitation caused longer cycles, because of a longer expansion phase (Figure 1). Autocorrelation and trends in the series were assessed with ARIMA models (Legendre and Legendre 1998) (ARIMA procedure, SAS Institute, Cary, NC). A t-test and a paired t-test were used to compare the duration of contraction and expansion phases within and between days with positive and negative ∆R. The t-tests included data from all 9 years. Relationships between $h$ and $v$ (MDS or ∆R) were assessed by linear regressions.

Climate and flow data were coupled with the respective daily MDS and ∆R (Downes et al. 1999, Deslauriers et al. 2003) with special routines written in SAS. For example, for each cycle, the mean temperature occurring during the contraction phase was coupled with the corresponding value of MDS. The association was first made for each tree and means were then calculated for each species and year.

Model description

The causal modeling used simple and partial correlations ($r$) to explain the relationships among descriptors, $h$ and $v$ based on two initial hypotheses. The descriptors consisted of sap flow, VPD, precipitation, soil water content and air temperature. For values of $v$ corresponding with MDS, $h$ was taken to be the duration of the contraction phase. In this case, the descriptors represent the weather conditions or the sum of sap flow occurring in that phase. For values of $v$ corresponding with ∆R+$\pm$, $h$ was taken to be the duration of the stem radius increment phase. In this case, the descriptors represent the weather conditions or the sum of sap flow occurring in that phase.

Initial hypotheses  The hypotheses define the causality links between $d$, $h$ and $v$ leading to the two models described below and correspond to the following correlations:

$$r_{dh} \neq 0$$  \hspace{1cm} (1)

$$r_{hv} \neq 0$$  \hspace{1cm} (2)

In the absence of significant correlations in Equations 1 and 2, neither model can be formulated because causal links are missing.

Models  Two models of causal relationships, deriving from the initial hypotheses, were defined as:

$\begin{align*}
d_i & \Rightarrow h_i \Rightarrow v_j \\
\text{Model 1} \\
d_i & \Rightarrow h_i \not\Rightarrow v_i \\
\text{Model 2}
\end{align*}$

where $d$ is a descriptor and $i$ represents a given phase. The arrows describe the possible interactions between $d$ and $v$ (representing MDS or ∆R) in the presence of possible interactions caused by $h$. In Model 1, the correlation between $d$ and $v$ is caused by $h$ (lack of causal relationship between $d$ and $v$), whereas in Model 2, the correlation between $d$ and $v$ is caused by both $d$ and $h$ (double cause).

Expectations of the models  Simple and partial regression analyses were performed between $d$, $h$ and $v$. A partial correlation coefficient measured the relationship between two variables (e.g., $d$ and $v$) controlling for the effect of a third (e.g., $h$) being constant at its mean and noted as $r_{d,h,b}$. According to the results, i.e., the expected values for the simple and partial coefficients, Model 1 or 2 was formulated for a given $d$. These expectations followed Legendre and Legendre (1998) and are described in Table 1. After verifying the initial hypotheses, Model 1 or 2 was selected by controlling each expectation and rejecting one or both models when the correlations did not correspond to the expectations.

The significance of the correlation coefficients and an estimate of the stability of the results were tested by confidence intervals obtained by the bootstrap procedure (Efron and Tib-
Table 1. Model expectations concerning the simple and partial correlations among descriptors (d), phase duration (h) and stem radial variation (v) (Legendre and Legendre 1998).

<table>
<thead>
<tr>
<th>Both Models</th>
<th>Model 1</th>
<th>Model 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>r_dh signif. ≠ 0</td>
<td>r_dh ≥ 1 r_dh</td>
<td>r_dh signif. ≠ 0</td>
</tr>
<tr>
<td>rvd signif. ≠ 0?</td>
<td>rvd × 1</td>
<td>rvd × 1</td>
</tr>
<tr>
<td>r_dh,v signif. ≠ 0</td>
<td>r_dh ≥ 1 r_dh</td>
<td>r_dh,v signif. ≠ 0</td>
</tr>
<tr>
<td>rvd,h signif. ≠ 0</td>
<td>rvd ≤ 2</td>
<td>rvd,h signif. ≠ 0</td>
</tr>
</tbody>
</table>

1 For Model 2, the model holds even if only one of these two simple correlations is not significant.

2 The phrase "r_dh,v not signif." means that the correlation is not necessarily significantly different from zero.

Results

Stem radial variations

The three species had similar time series of ΔR variations from May to October 2001 (Figure 2d, 2001 was taken as an example) with alternating periods of positive and negative variations. During June and July (growth period), the amplitude of ΔR ranged from −50 to 250 µm for all species. In August, ΔR– occurred more frequently when the season's radial growth was almost complete (Figures 2c and 2d). These series were stationary (homoscedastic), with no probability of autocorrelation within the previous six cycles (lag-6, P < 0.01). Compared with the time series of ΔR variations, the time series characterizing MDS were less similar between species and were frequently non-stationary, because the range of variations changed from 0 to 50 µm in June–July to 0 to 100 µm in August, when stem growth was close to ending (Figure 2e).

Annual and intra-annual radial growth

To evaluate the accuracy of the dendrometer measurements, the total radial increment calculated with ΔR was compared with the widths of tree rings formed from 1996 to 2004 (Figures 3a–c). For each tree, no significant difference was found between the cumulated ΔR and tree-ring width (paired t-test, P > 0.1). Ring-widths differed according to the position around the stem, but the cumulative ΔR was generally within the range of variation of the ring width for P. abies and L. decidua (Figures 3a and 3b). For P. cembra in some years, however, the cumulated ΔR was outside the range of variation of tree-ring measurement, even when no significant difference was found in either tree (paired t-test, P = 0.67 and P = 0.26 for trees 1 and 2, respectively). When associated with measurement of tree-ring formation, the cumulated sum of ΔR showed similar intra-annual radial growth (Figures 3d and 3e). In 2004, for example, the ΔR rate of increase in June and July was similar to that of five other trees of the same age and dimensions.

Phase duration

The time of onset of each diurnal phase was calculated and averaged over 9 years (Table 2). For both P. abies and L. decidua, the stem diameter contraction phase started on average at 1030 (± 3) h and continued until 1800–1900 (± 2) h, when the diameter expansion began. Pinus cembra showed a delay of about 1 h in the onset of expansion compared with the other species. When it occurred, the stem increment phase started between 2200 and 2400 (± 3) h. The stem cycles were divided in two groups: cycles < 28 h were considered as regular circadian diurnal; and cycles > 28 h were considered as long cycles (Figure 1, Table 2). The main difference characterizing the long cycles was the longer expansion phase lasting 34–40 h. There were about five (± 2) long cycles per month from May to September, corresponding with rain events (Figures 2a, c and d). The highest ΔR+ values were calculated during long cycles.

To understand the difference between the diurnal cycles with ΔR + and those with ΔR −, the duration of the contraction
and expansion phases were compared (Figure 4). When a cycle with $\Delta R^-$ occurred, both contraction and expansion phases lasted about 12 h, with no significant difference between them for all species (paired $t$-test, $P > 0.05$). In 1999 and 2003, the higher differences were the result of a small number of $\Delta R^-$ ($n < 5$). In contrast, when a $\Delta R^+$ occurred, the contraction phase was significantly shorter than the expansion phase in all species (paired $t$-test, $P < 0.001$). Compared with the cycle with $\Delta R^+$, the number of hours of contraction were significantly higher and the number of hours of expansion were significantly lower for the cycle with $\Delta R^-$ ($t$-test, $P < 0.001$). The cycle with $\Delta R^+$ therefore occurred more often when there were unbalanced cycles with 6–8 h of contraction and 16–18 h of expansion (Figure 4).

Relationship between duration and amplitude

The duration of the contraction and expansion phases influenced MDS and $\Delta R$, respectively (Figures 5 and 6). In all species, the MDS (absolute values) increased linearly with duration ($P < 0.001$, Figure 4). Log transformations were performed because variation in MDS increased with duration. When the duration of stem contraction increased, MDS was observed to increase proportionally more in $P. abies$ than in $L. decidua$ and $P. cembra$, as shown by the regression slopes (Figure 5). The duration of the expansion phase influenced the $\Delta R$ in all species. Linear regressions showed positives slopes ($P < 0.01$), with higher rates of change in $L. decidua$ and lower rates of change in $P. cembra$ (Figure 6).

Models of causal relationship

MDS

The simple and partial correlation results demonstrate that the sap flow and VPD data supported causal Model 2 (Table 3, Figure 7). The MDS of all species was positively correlated with sap flow ($r_{dv}$), with correlation coefficients varying between 0.65 for $P. abies$ and 0.78 for $P. cembra$, and, according to Model 2, these correlations were caused by both duration of the contraction phase and sap flow. The simple correlations between MDS and VPD were significant and varied between 0.48 and 0.69, depending on species. Except for $L. decidua$, the partial correlations ($r_{dh.v}$ and $r_{dh.h}$) indicated that correlation was caused by VPD and phase duration. For $L. decidua$, the partial correlation $r_{dh.v}$ was not significant, which did not fulfil the conditions for Model 2.

The initial hypotheses were not fulfilled for precipitation and soil water content because the simple correlations $r_{dh}$ were not significant (Figure 7). During a rainy period, the contraction phase normally lasted only a few hours or was absent, leading to a long cycle. For air temperature, the partial correlations $r_{dh.h}$ were not significant, which does not fulfil the expectations of Model 1 or 2 (Figure 7). Neither model could therefore be formulated between precipitation, air temperature or soil water content and contraction phase duration or MDS.

Positive stem radius change

According to the model results, sap flow or precipitation fulfilled the prerequisites and expectation of Model 2, whereas air temperature and soil water content fulfilled the prerequisites and expectation of Model 1 (Table 3, Figure 7). The correlations and partial correlations between VPD, phase duration and $\Delta R^+$ supported neither model (Table 2, Figure 7). Non-significant or low simple correlations...
Figure 3. Left: Tree-ring width (mm) measured in four cardinal directions for Tree 1 (●) and Tree 2 (○) of each species associated with the corresponding cumulated stem radial variation ($\Delta R$; mm, ★, ◦) from 1996 to 2004. Right: Cumulated increase in $\Delta R$ (black line) and in tree-ring growth (●) during the 2004 growing season.

Table 2. Timing characteristics and standard deviation (in brackets) of the contraction (1), expansion (2) and growth (3) phases of diurnal and long cycles of variation in stem diameter in *Picea abies*, *Larix decidua* and *Pinus cembra*. The times of phase onset and mean duration (hours) were calculated for the months of June and July 1996–2004.

<table>
<thead>
<tr>
<th>Species</th>
<th>Phase</th>
<th>Time of onset (h)</th>
<th>Mean duration of diurnal cycles (h)</th>
<th>Mean duration of long cycles (h)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Picea abies</em></td>
<td>1</td>
<td>1018 (3.48)</td>
<td>7.59 (3.29)</td>
<td>7.35 (3.24)</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>1835 (2.10)</td>
<td>14.55 (4.00)</td>
<td>40.18 (19.50)</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>2252 (3.11)</td>
<td>11.23 (5.26)</td>
<td>35.11 (20.18)</td>
</tr>
<tr>
<td></td>
<td>Cycle</td>
<td></td>
<td>22.49 (3.18)</td>
<td>47.45 (18.43)</td>
</tr>
<tr>
<td><em>Larix decidua</em></td>
<td>1</td>
<td>1044 (3.51)</td>
<td>8.13 (3.06)</td>
<td>7.47 (4.04)</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>1906 (2.18)</td>
<td>14.54 (3.43)</td>
<td>36.26 (19.29)</td>
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<td></td>
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<td>11.01 (4.55)</td>
<td>32.95 (20.56)</td>
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<tr>
<td></td>
<td>Cycle</td>
<td></td>
<td>23.02 (3.16)</td>
<td>44.05 (18.10)</td>
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<tr>
<td><em>Pinus cembra</em></td>
<td>1</td>
<td>1027 (3.33)</td>
<td>9.19 (3.41)</td>
<td>9.40 (5.55)</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>2026 (2.43)</td>
<td>13.28 (3.52)</td>
<td>34.44 (17.32)</td>
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<td>0008 (3.00)</td>
<td>10.22 (5.05)</td>
<td>31.31 (17.16)</td>
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<tr>
<td></td>
<td>Cycle</td>
<td></td>
<td>22.39 (3.17)</td>
<td>44.23 (15.57)</td>
</tr>
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</table>
were found between sap flow and \( \Delta R \). The partial correlations for \( L. \) decidua and \( P. \) abies indicated that \( r_{dv} \) corresponds to two opposing effects: a positive effect of sap flow on the duration of the stem radius increment phase \( (r_{dh,v}) \) and a negative effect of sap flow on \( \Delta R \) \( (r_{dv,h}) \). For \( P. \) cembra, the expectations of Model 2 were not fulfilled because \( r_{dv,h} \) was not significant. For precipitation, all partial correlations were significant, fulfilling the expectations of Model 2 for all species. The partial correlations \( r_{dv,v} \) and \( r_{dv,h} \) corresponded to two positive effects of precipitation: a positive effect on phase duration \( (r_{dv,v}) \) and also on \( \Delta R \) \( (r_{dv,h}) \). The simple correlation \( (r_{dv}) \) varying from 0.36 for \( P. \) cembra to 0.44 for \( L. \) decidua was therefore caused by both precipitation and duration of the stem radius increment phase.

The simple correlation \( (r_{dh}) \) between \( \Delta R \) and air temperature varied between –0.27 for \( P. \) cembra and –0.38 for \( P. \) abies. However, these correlations were caused by phase duration only (i.e., lack of causal relationship). Therefore, an increase in temperature shortened the duration, which in turn decreased \( \Delta R \). The simple correlation \( (r_{dh}) \) between soil water content and \( \Delta R \) was caused only by phase duration: an increase in soil water content increased the phase duration and, in turn, \( \Delta R \).

**Discussion**

The amplitude of stem radius variation, calculated as MDS and \( \Delta R \), was highly dependent on phase duration. From spring to autumn, the timing of the diurnal dynamics of stem tissue

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**Figure 4.** Duration of contraction and expansion phases for the diurnal cycles leading to negative (in gray) or positive (in black) stem radial variation \( (\Delta R) \). The standard errors (not shown) varied between 2 and 3 h. Paired \( t \)-tests were used to compare the duration of contraction and expansion within the diurnal cycle with \( \Delta R \)– (gray uppercase letters) or \( \Delta R \) (black uppercase letters). The \( t \)-tests were used to compare the duration of contraction (a and b) or the duration of expansion between positive and negative \( \Delta R \) (y and z). Different uppercase letters indicate significant differences \( (P < 0.05) \) between series.

**Figure 5.** Relationship between maximum daily shrinkage (\( \log(MDS) \)) and phase duration (\( \log(h) \)) in \( P. \) cembra, \( L. \) decidua and \( P. \) abies in June–July 1996–2004. Only diurnal cycles are illustrated. All regressions were significant at \( P < 0.01 \). Thick, thin and broken lines represent the regression, 95% confidence limits and 95% confidence bands, respectively.
water depletion and replenishment is subject to constant changes and varies as a function of environmental conditions, transpiration and sap flow (Zweifel and Häsler 2001, Perämäki et al. 2001). Despite this variability, the possibility of measuring a positive or negative $\Delta R$ was associated with the timing and duration of the diurnal cycles resulting in balanced (~12/12 h) or unbalanced (~7/17 h) cycles. Given that both components are dependent, a climatic or physiological factor acting on one component can influence the other.

Causal effect of water and temperature on MDS

In June and July, the contraction phase started on average between 1000 and 1100 (± 3) h, with the latest onset observed in *P. cembra*. The onset of contraction was later (4–5 h) than in young trees (Steppe et al. 2006), suggesting that conditions for cell expansion in large trees are met not only during the night but also early in the day. For a subalpine *Picea abies*, Zweifel and Häsler (2001) reported onset of the phase of stem diameter contraction at 0900 h at the base of the stem, on a sunny July day. The onset of stem contraction and sap flow at the stem base both show a time lag in response to the onset of transpiration at the top of the tree, creating a peristaltic wave of contraction along the stem (Wronski et al. 1985, Wullschleger et al. 1998, Perämäki et al. 2001) that varies as a function of the amount of stored water used (Ford et al. 2004). Diameter changes along the stem correspond to a depletion of stored water through transpiration (Zweifel and Häsler 2001). At the base of the stem, the MDS rate of change was lower for *L. decidua* and *P. cembra* compared with *P. abies*. Although *L. decidua* has a higher transpiration rate and sap flow than *P. cembra* and *P. abies*, it can support high water losses because it has a higher water uptake capacity (Anfodillo et al. 1998). *Larix decidua* shows a higher root-to-shoot water potential gradient achieved through osmoregulation, which leads to reduced stem dehydration (Badalotti et al. 2000). Both *P. abies* and *P. cembra* have a general water-saving strategy with higher minimum stem water potentials than *L. decidua* (Anfodillo et al. 1998). However, *P. abies* had a higher MDS rate of change than *P. cembra* because of a higher sap flow rate. Thus, in the species studied, the changes in MDS confirmed that, at the alpine treeline, *P. cembra* is the most water-saving species (Tranquillini 1979).

Only sap flow and VPD directly affected the duration of the contraction phase. For all species, these results are in agreement with the finding that sap flow is coupled with transpiration (Steppe et al. 2006). Sap flow and VPD also influenced

<table>
<thead>
<tr>
<th>Descriptors</th>
<th>MDS</th>
<th></th>
<th>Model fit</th>
<th>MDS</th>
<th></th>
<th>Model fit</th>
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<tbody>
<tr>
<td>Sap flow</td>
<td>Yes</td>
<td>Yes</td>
<td>2</td>
<td>Yes</td>
<td>Yes</td>
<td>2*</td>
</tr>
<tr>
<td>Vapor pressure deficit</td>
<td>Yes</td>
<td>Yes</td>
<td>2**</td>
<td>Yes</td>
<td>Yes</td>
<td>No fit</td>
</tr>
<tr>
<td>Precipitation</td>
<td>No</td>
<td>Yes</td>
<td>-</td>
<td>Yes</td>
<td>Yes</td>
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<tr>
<td>Soil water content</td>
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<td>Yes</td>
<td>-</td>
<td>Yes</td>
<td>Yes</td>
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<tr>
<td>Air temperature</td>
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<td>Yes</td>
<td>No fit</td>
<td>Yes</td>
<td>Yes</td>
<td>1</td>
</tr>
</tbody>
</table>

No fit for *P. cembra* and **L. decidua.
MDS, which agrees with other results with *P. abies* (Herzog et al. 1995). However, these high correlations were also dependent on phase duration (i.e., Model 2) and not just on sap flow or VPD. In the morning, sap flow increased with VPD, but reached a maximum of 4–5 hPa, for all studied species, and then remained stable (saturation effect) (Anfodillo et al. 1998). Maximum sap flow is related to the hydraulic resistance of the whole path (roots–leaves) and the capacity to lower the minimum leaf water potential, e.g., through osmoregulation. The nonlinearity of the relationship between sap flow and VPD makes it necessary to consider the duration of the contraction phase in the relationship with MDS because the rate of increase in sap flow decreases as long as stem contraction continues.

*Causal effects of water and temperature on ΔR*

In all species, when ΔR+ occurred, stem radial expansion started around midnight (± 3h) and lasted for 11 (± 5) h in June and July, which is similar to the timing observed for *A. balsamea* in Canada (Deslauriers et al. 2003). In young *Fagus sylvatica* L., radial stem growth is modeled to occur mainly during the night when the pressure potential in the stem stor-

**Figure 7.** Correlation matrix representing simple (white background) and partial (gray background) coefficients among descriptors (*d*), phase duration (*h*), and radial variation (*v*). At left, *v* is represented by maximum daily shrinkage (MDS) and at right *v* is represented by stem radial variation (ΔR). The vertical bars indicate the 95% distribution of the correlation coefficients. Correlations are not significant when bars cross zero. continued overleaf.
age compartment (outside xylem) exceeds a wall-yielding threshold value (Steppe et al. 2006). In mature conifers, swelling usually lasts longer, hence radial growth during the morning cannot be excluded. In the studied species, *P. cembra* had the smallest change in ∆R because of higher minimum water potential and lower stem rehydration (Anfodillo et al. 1998). Although having smaller changes in MDS, the change in ∆R was larger for *L. decidua* because of its higher water uptake capacity and overall growth.

The results of the causal relationships suggest a new physiological interpretation of the growth–climate relationship obtained from daily dendrometer measurements. The variation in stem diameter includes several components (Daudet et al. 2005), the most important being irreversible radial growth and reversible living-cell dehydration–rehydration. In conifers, the tissue water-content-related stem diameter variations (i.e., when the growth trend is removed) are largely determined by soil water availability and atmospheric VPD (Zweifel et al. 2005). However, air and soil conditions explain both the water-related change in stem radius and ∆R, considered as an estimate of stem growth. Phase duration, taken as an indicator of the reversible changes in stem radius, depends mainly on transpiration and sap flow (Herzog et al. 1995). Radial growth increments are greater in longer expansion phases, which obscures any relationship between ∆R and other variables.

Our results demonstrate that precipitation has two main effects: a direct effect on ∆R and an indirect effect through an effect on *h* as a result of the nonlinearity of the physiological responses to climatic factors. The main effect of precipitation is to enhance the water status in the stem, creating high water potentials that favor cell enlargement (Proseus and Boyer 2005, Steppe et al. 2006), and hence, positive correlations with precipitation are found in different species and environments (Downes et al. 1999, Tardif et al. 2001, Deslauriers et al. 2003, Bouriaud et al. 2005). When including long cycles in the analysis, the simple correlations between ∆R and precipitation increase from about 0.40 (Figure 7) to 0.60 (data not shown), because long cycles correspond to higher ∆R during heavy rain events (Figure 2).

Sap flow had opposite effects on the stem radius increment phase duration and ∆R+: sap flow was positively correlated with duration at constant ∆R (*r*<sub>dl,h</sub>), whereas it was negatively correlated with ∆R at constant duration (*r*<sub>dl,d</sub>). The ∆R reflects replenishment of internal water stores in addition to irreversible stem growth. The longest phases of expansion occurred when total sap flow was highest (i.e., cumulated sum). Therefore, when the variation explained by *h* is removed, a reduction in sap flow at night leads to an increase in ∆R in *P. abies* and *L. decidua* because sap flow is predictive of the meristem water potential: if sap flow is higher, a lower water potential.
should occur within the living cells. Steppe et al. (2006) observed an increase in stem diameter in *Fagus sylvatica* L. after a decrease in transpiration rate and a subsequent decrease in sap flow at the stem base. Irreversible changes in cell walls are expected to occur when water in cambial tissue is replenished (Abe et al. 2003) and when nighttime stem water potential exceeds the water potential of storage compartments (Herzog et al. 1995, Zweifel and Häslé 2001). *Pinus cembra* showed no partial correlation between irreversible growth increment and sap flow, probably because the variation in water potential of cambial cells is much less than in the other species.

The negative correlation between $\Delta R$ and air temperature was caused by the effect of temperature on $h$ and does not correspond, on a daily scale, with a direct physiological effect on tree growth mediated by an effect on metabolic activity. These results support the hypothesis that $\Delta R$ mainly reflects radial growth, dependent on tissue water status, and in a minor way on changes in C metabolism (Daudet et al. 2005, Zweifl et al. 2006). As suggested by Tardif et al. (2001), the negative relationship between $\Delta R$ and temperature is probably due to a negative effect of transpiration on radial expansion. Through transpiration, higher day and night temperatures lead to a balanced cycle that reduces $\Delta R$.

In conclusion, we demonstrated that the duration of stem water storage tissue refilling explains a high proportion of $\Delta R$. When correlations of $\Delta R$ with sap flux and climate are considered, duration removes a proportion of the reversible stem contraction effects and helps to discriminate better between the factors influencing $\Delta R$. The growth–climate relationships found based on dendrometer measurements were not always in agreement with other results. In the Alps, for example, a positive correlation between ring width and June–July temperature was found (Carrer and Urbini 2004, Oberhuber 2004), whereas in our study, negative temperature effects, associated with phase duration, were observed. Therefore, at a short time-scale, growth–climate relationships should be interpreted as a function of the process measured, which, in this case, is highly water-dependent.

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