To determine the relationship between phloem transport and changes in phloem water content, we measured temporal and spatial variations in water content and sucrose, glucose and fructose concentrations in phloem samples and phloem exudates of 70- and 30-year-old Norway spruce trees (*Picea abies* (L.) Karst.). Large temporal and spatial variations in phloem water content (1.4–2.6 mg mgdw⁻¹) and phloem total sugar concentration (31–70 mg g dw⁻¹) paralleled each other (*r*² = 0.83, *P* < 0.0001 for the temporal profile and *r*² = 0.96, *P* < 0.008 for the spatial profile), indicating that phloem water content depends on the total amount of sugar to be transferred. Changes in phloem water content were unrelated to changes in bark thickness. Maximum changes in phloem water content calculated from dendrometer readings were only 8–11% of the maximum measured changes in phloem water content, indicating that reversible changes in bark thickness did not reflect changes in internal water relations.

We also studied the relationship between xylem sap velocity and changes in bark thickness in 70-year-old trees during summer 1999 and winter 1999–2000. Sap flow occurred sporadically throughout the winter, but there was no relationship between bark shrinkage or swelling and sap velocity. In winter, mean daily xylem sap velocity was significantly correlated with mean daily vapor pressure deficit and air temperature (*P* < 0.0001, in both cases). Changes in bark thickness corresponded with both short- and long-term changes in relative humidity, in both winter and summer. Under controlled conditions at > 0 °C, changes in relative humidity alone caused changes in thickness of boiled bark samples. Because living bark of Norway spruce trees contains large areas with crushed and dead sieve cell zones—up to 24% of the bark is air-filled space—we suggest that this space can compensate for volume changes in living phloem cells independently of total tissue water content. We conclude that changes in bark thickness are not indicative of changes in either phloem water capacitance or xylem sap flow.

Keywords: carbohydrates, phloem transport, stem radius variation.

Reversible changes in bark thickness are well documented. In summer, these changes in bark thickness show a clear diurnal oscillation with shrinkage during the day and swelling overnight. On cloudy or rainy days, the rhythm becomes more irregular and swelling increases. Because diurnal changes in bark thickness typically follow changes in leaf and xylem water potentials (Lassoie 1973, Waring et al. 1979, McBurney and Costigan 1984), it has been postulated that they are caused by the exchange of water between xylem and phloem, driven by changes in xylem water potential during transpiration (Dobbs and Scott 1971, Molz et al. 1973, Jarvis 1975, Parlange et al. 1975). Molz and Peterson (1974) showed that the rate of water exchange between the xylem and its surrounding phloem is temperature-dependent, indicating that the peripheral tissues act as a site of water storage for the whole tree. Models of phloem or whole-plant water capacitance have been proposed (Molz et al. 1973, Parlange et al. 1975, Zweifel et al. 2000).

Lövdahl and Odin (1992) induced fluctuations in bark thickness of chamber-grown Norway spruce seedlings (*Picea abies* (L.) Karst.) by adjusting temperature and air relative humidity. They showed, however, that the daily changes in stem diameter remain unaffected if all needles were removed, and concluded that changes in bark thickness reflect the hygroscopic behavior of tree bark and are independent of the transpiration rate. Apart from the diurnal changes in bark thickness during summer, unexplained fluctuations in stem thickness also occur in winter, even at temperatures above the freezing point. Loris et al. (1999) proposed that winter fluctuations in stem thickness can serve as an indicator of water stress that occurs when soil water is frozen and cuticular and peridermal transpiration increase in response to above freezing air temperatures. Loris et al. (1999) concluded that the changes in stem thickness are an indication of water transfer along an osmotic gradient, over the whole tree stem and over time.

The bark of tree stems and branches is highly differentiated, consisting of meristems, conductive and nonconductive phloem and cortex (Kozlowski 1992). An understanding of changes in phloem water content requires consideration not
only of the effects mediated by the xylem but also those arising in the phloem itself. According to the pressure–mass flow theory of phloem transport, assimilation products in the phloem cause mass flow as a consequence of the osmotic pressure that they generate (Van Bel 1993). Therefore, changes in bark water content (and the resulting changes in bark thickness) need to be considered in the context of (i) changes in water content in the phloem tissue resulting from mechanisms affecting water capacitance, (ii) phloem transport and (iii) the hygroscopic response to air humidity.

Because of its potential use as an index of whole-plant water movement and plant vitality (e.g., Loris et al. 1999, Zweifel et al. 2000), measurements of bark water content may be of fundamental interest in studies of plant development and plant ecology. However, the driving forces and their relative impact on changes in bark water content need to be clarified. Therefore, we studied relationships between directly measured phloem water content and phloem carbohydrate concentration. We tested the hypothesis that the phloem water content mainly depends on the amount of total sugar to be transferred. We examined the relationship between changes in phloem water content and changes in bark thickness to assess the relevance of the phloem water capacitance model.

We also investigated the effects of meteorological conditions on changes in bark thickness. Direct measurements of phloem water content led us to doubt the relevance of the capacitance model to the explanation of the underlying driving force. We found that temporal variation in directly measured phloem water content was strongly correlated with phloem sugar concentration in accordance with the basic mechanisms of phloem transport, i.e., phloem water content depends on the amount of carbohydrate to be transferred (Van Bel 1995). However, changes in phloem water content were larger than, and out of phase with, changes in bark thickness. Therefore, we tested the hypothesis that changes in bark thickness at temperatures > 0 °C can be explained solely by changes in relative humidity. Furthermore, the absence of a relationship between directly measured phloem water content and bark thickness led us to examine whether sufficient intercellular air space exists to accommodate changes in phloem water content without corresponding changes in bark thickness.

Materials and methods

Experimental site and plant material

Phloem measurements were made on apparently healthy Norway spruce trees (Picea abies (L.) Karst), aged about 70 and 30 years. The 70-year-old trees were growing in a homogeneous managed stand of Norway spruce in association with some beech (Fagus sylvatica L.) and Douglas-fir (Pseudotsuga menziesii Mirb.) trees. The study plot is located in Unterehrendingen, Switzerland at an elevation of 470 m. The site has a well drained, sandy-loamy acidic brown soil, developed on upper sea molasses, which is a Miocene bedrock. Meteorological data were obtained from a station located at an open field site 300 m from the research plot. Measurements on the 30-year-old trees were made in our experimental garden in Birmensdorf, Switzerland, 540 m above sea level. Meteorological data for this study site were obtained from a station located at an open field site 150 m from the investigated trees.

Xylem measurements were made on 12 of the 70-year-old Norway spruce trees during summer 1999 and winter 1999–2000. The 12 trees had a mean diameter of about 0.37 m at breast height. Mean annual air temperature and relative air humidity during the experimental year were 9.8 °C and 78%, respectively. Annual precipitation was 1294 mm. Meteorological data for the winter were obtained from an official MeteoSwiss-station located in Buchs-Suhr, 6 km from the study site, whereas data for the summer period were obtained from the station located 300 m from the study site.

Collection of bark samples and extraction of bark carbohydrates

Bark samples were taken with an increment puncher (Forster et al. 2000), consisting of a hollow needle with a diameter of 2.5 mm. The needle was punched into the stem, producing core lengths of about 10 mm. Wood cores were taken with a 10-mm-diameter increment borer and cut into 5-mm segments. To extract carbohydrates, bark samples were frozen in liquid nitrogen immediately after collection. Subsequently, the cortex and xylem were excised leaving only the conductive and nonconductive phloem tissue. The samples were lyophilized and then homogenized with a microdismembrator (Braun AG, Melsungen, Germany) in 2 ml of double-distilled water for 1 min. Each homogenate was placed in a 6-ml vial and centrifuged at 2500 g for 15 min. The pellets were re-extracted with an additional 2 ml of double-distilled water and centrifuged again. The pooled supernatants were dried in a vacuum centrifuge, re-extracted with 3–5 ml of double-distilled water and filtered over a cellulose membrane (0.45 µm). The samples were stored on ice between steps. Total water content of the samples was calculated as the difference between fresh weight and dry weight after lyophilization.

Phloem exudate was collected by the EDTA technique described by Schneider et al. (1996). After harvest, the samples were washed in double-distilled water to exclude contamination with xylem sap. Subsequently, the samples were incubated in 10-ml vials containing 2 ml of exudation solution (10 mM EDTA and 0.015 mM chloramphenicol at pH 7.0). The exudation was completed in 5 h at room temperature (data not shown). After exudation the remaining tissues were lyophilized and processed as previously described.

Calculation of water content and sugar concentration

Spatial variations in amounts of water and sugar along and around the stems were expressed as quantities per cylindrical sample. For time series, amounts were always measured in samples taken at breast height and expressed per unit dry weight (dw) to minimize the anatomical effect of irregular phloem thickness (Figure 1).
High performance liquid chromatography analysis of sugars

Sugars were chromatographed on a 250 × 4.1 mm RCX-10 column (Hamilton, Reno, NV) at room temperature. The injected sample amount was 10 µl. The eluent was water containing 75 mM NaOH and 3.75 mM sodium acetate with a flow rate of 0.4 ml min⁻¹. Detection was by a pulsed amperometric detector (PAD, Coulochem II, ESA, Bedford, MA). The pulse potentials \(E_1 = 200\) mV, \(t_1 = 500\) ms; \(E_2 = 700\) mV, \(t_2 = 100\) ms; and \(E_3 = -900\) mV, \(t_3 = 300\) ms. System operations and data management were made with the Turbochrom software (Version 4.1, Perkin Elmer, Norwalk, CT).

Fluctuations in bark thickness

Fluctuations in bark thickness were recorded with point dendrometers (resolution = 3.7 µm), consisting of a precision displacement transducer clamped on a frame of stainless steel. Each frame was attached on the south side of a stem about 2 m above ground with screws drilled into the stem to a depth of 50 mm. Drill pits for anchoring the frame and the contact point of the sensor were 60 mm apart (Herzog et al. 1995). The contact point was set on the dead layer of the bark but 2 to 6 mm below the surface, to minimize bias caused by hygroscopic bark swelling and shrinkage (Herzog et al. 1995). Temperature sensitivity was linearly correlated with air temperature, with an increase of 1 °C causing a mean contraction of 1.4 µm (Zweifel and Häsler 2000). The fluctuations were recorded every 5 min and stored as 15-min means.

Xylem sap velocity measurements

We measured sap velocity with Granier-type sensors (TDP-80, Dynamax, Houston, TX). Granier-type sensors consist of two needles, both implanted in the sapwood of the tree, with the upper needle containing an electric heater (Granier 1985). We attached one sensor per tree to the southwest side of the stem about 2 m above ground. Xylem sap velocity was recorded every 5 min and stored as 15-min means.

Climate chamber experiments

Dendrometer measurements were made on small bark chips (1 cm²) where the contact point was set 2 to 6 mm below the surface as described above. The cortex was removed from each chip and the remaining tissues were boiled in water for 3 min to break open the cell walls and wash out the cell sap. The bark chips were equilibrated under the experimental conditions and then glued to a metal plate. Wood samples were also taken from the sapwood area. Air humidity was controlled according to a diurnal rhythm typical of a clear weather period (42 to 95% relative humidity). The temperature was kept constant at 20 °C.

Estimation of the air-filled intercellular space

To estimate the air-filled intercellular space of living bark samples, we used bark cores taken with a 5-mm-diameter increment borer. Immediately after collection, the samples were roughly separated into: nonconductive phloem, conductive phloem and cortex. The xylem was discarded. After weighing, we measured core length and diameter to estimate the volume of each core. These measurements were performed on the shadow of the cores produced by an overhead projector, enabling a 10-fold magnification. Measurements of the shadow were carried out with a vernier caliper. Subsequently, the cores were degassed for 3 min in a water bottle under vacuum, to exchange intercellular air with water. The cores were then weighed and core length and diameter were remeasured. Samples were then dried in a desiccator to constant weight.

Results

Sugar distribution in phloem and hydroactive xylem

Simultaneous collection (August 24, 2000) of bark samples from six trees showed that 71% (standard deviation = 7.5%) of the total sugar concentration was located in the phloem exudates and 29% remained in the tissue in both 30- and 70-year-old trees (Figure 2). The higher amount of total sugar in phloem exudates than in bark tissue was associated with a higher sucrose concentration in the exudate because fructose and glucose concentrations were similar in the exudates and the remaining tissue. In the adjacent xylem, sugar concentration and relative water content decreased dramatically in the first 15% of sapwood depth (Figure 3).
Relationship between water content and sugar concentration

In both 30- and 70-year-old trees, temporal variation in sugar concentration of phloem exudates paralleled that in water content (Figures 4a and 4b), resulting in a strong, linear correlation \((r^2 = 0.83, P < 0.0001\) and \(r^2 = 0.76, P < 0.0001\), for the 30- and 70-year-old trees, respectively). The sugar concentration remaining in bark tissue also showed temporal variations, but the changes were more or less inversely correlated with the changes in sugar concentration of the phloem exudates (Figure 5).

Spatial variations in sugar concentration and water content were measured at 0900 and 1600 h along the entire branch-free stem length (20 m) of a 70-year-old tree (Figure 6). The sugar concentration of phloem exudates increased with stem height, by 44 and 33% at 0900 and 1600 h, respectively. There was a
significant correlation between phloem sugar concentration and water content \( (r^2 = 0.95, P < 0.015 \) and \( r^2 = 0.96, P < 0.008, \) respectively). These results were verified by measurements at 1, 3.5 and 7 m on a 30-year-old tree over a branch-free stem length of 7 m. In this tree, sugar concentration of phloem exudates increased with stem height by 22 and 17% at 0900 and 1600 h, respectively, corresponding with increases in water content at 3.5 and 7 m.

During a 6-week period between January 27 and March 10, we measured the total sugar concentration (glucose, fructose, sucrose and raffinose) in the phloem of 15 Norway spruce trees. During this period, glucose and fructose concentrations decreased and sucrose concentration increased (data not shown). Sugar concentrations in the bark tissue remained constant over the measurement period, resulting in a significant positive correlation between absolute amounts of sugar and water (Figure 7).

**Relationship between bark thickness and water content**

In both 30- and 70-year-old trees, the reversible changes in bark thickness showed a diurnal oscillation with daytime shrinkage and nighttime swelling. Xylem sap flow during the daytime was high (see Figure 11). Changes in bark thickness tracked changes in relative air humidity with a lag of 2 to 3 h (Figures 8a, 9a and 10a).

We observed large temporal variations in phloem water content that varied among trees and were higher than predicted by the dendrometer recordings (Figures 8–10) (volume changes calculated from dendrometer recordings were only 8.0–10.8% of the changes in directly measured phloem water content). For the 30-year-old tree Lisa (Figure 8), an overall decrease in phloem water content was observed over the period of investigation, but no diurnal rhythm was apparent. The 70-year-old tree Harwa (Figure 9) showed a trend of decreasing water content during the day and increasing water content during the night, but the signal was weak because of rapid and irregular...
changes. The 30-year-old tree Michael (Figure 10) showed a progressive increase in water content during the afternoon and night that was followed by a rapid decrease in the morning.

Changes in bark thickness and xylem sap velocity during summer

Because dendrometer readings represent stem growth as well as reversible changes in bark thickness, the relationships between relative humidity and bark thickness are presented here for a period when stem growth was nearly completed (August 12–20, 1999, Figure 11). In general, all stems showed the same fluctuations in bark thickness and xylem sap velocity, differing only in the amplitude of the changes.

The time course of reversible bark thickness changes followed the changes in relative humidity with a lag of 2 to 3 h. However, the ratio between changes in relative humidity and changes in bark thickness varied between periods of clear and sunny weather and periods followed by a rainy day. Relative humidity and vapor pressure deficit (VPD) were correlated because of the narrow temperature range within the experimental period. Therefore, the strong relationship between sap velocity and VPD (above a threshold of about 300 Pa in Figure 11b) implies a strong relationship between sap velocity and relative air humidity. However, this relationship did not always hold, as indicated by results for the night of August 18–19 when there was a decrease in relative air humidity and a decrease in bark thickness, but no sap flow was detected.

Changes in bark thickness and xylem sap velocity during winter

The period from November 7 to February 29, when trees showed no diurnal rhythm in stem thickness, was selected for analysis of relationships between meteorological conditions, bark thickness fluctuations and sap velocity during winter. Maximum fluctuations in bark thickness of individual trees, including frost-induced changes, were 100 to 500% greater than those of the previous summer (data not shown). In general, all stems showed similar bark thickness fluctuations, differing only in amplitude. Frost shrinkage and thaw expansion, which are indicated by a sudden reduction in bark thickness and a rapid expansion, respectively, occurred at air temperatures below the freezing point, e.g., between January 21 and January 30 (Figure 12).

During winter 1999–2000, considerable sap flow was detected during the night, corresponding to a lag of up to 12 h with rising VPD. Daily xylem sap velocity, however, was significantly correlated with mean daily VPD and air temperature ($P < 0.0001$, each). For these analyses, data for all trees were used for periods with air temperatures $> 0 \, ^\circ C$.

In contrast to the summer measurements, changes during the winter in xylem sap velocity were unrelated to changes in bark thickness (Figure 13a). However, as in summer, changes in bark thickness tracked, with a lag, the short- and long-term
trends in relative humidity and air temperature ($T_{\text{air}} > 0 \, ^\circ\text{C}$) (Figures 13b and 13d).

**Climate chamber experiments**

In the climate chamber experiments, changes in relative air humidity induced a comparable change in the thickness of entire bark chips (Figure 14a), as well as in the partitioned and boiled chips (phloem and cortex, Figures 14b and 14c). As in living trees, changes in bark chip thickness followed changes in relative air humidity with a lag of about 2 to 3 h, independently of whether the entire bark, the boiled phloem or the cortical tissue was measured. The amplitude of the changes varied among samples from 80 to 200 µm, which is comparable with the extent of change observed in bark of living trees. Sapwood samples responded to changes in relative humidity (± 80 µm), but not to changes in air temperature (data not shown).

**Air-filled intercellular space and reversible water uptake**

Replacement of intercellular air with water led to an increase in total core weight of 34.6% (SE ± 3.2%) in the conductive phloem and 47.7% (SE ± 12.3%) in the nonconductive phloem (Table 1), whereas in both tissues the core volumes remained unaffected. This water uptake resulted in a change in mean water content from 59.2% per unit fresh weight to 93.8% per unit fresh weight. This range is greater than the range of all water contents measured in trees Harwa and Michael during the experiments (see Figures 9 and 10).

The differences correspond to an air-filled space of 24.3% (SE ± 2.4%) for the conductive phloem and an air-filled space of 23.2% (SE ± 4.8%) for the nonconductive phloem. Further water uptake led to an increase in core volume (Table 1). This
reversible effect was most pronounced in the cortex, followed by the adjacent nonconductive phloem and the conductive phloem.

**Discussion**

Assimilation products are transferred down the stem by mass flow of water and carbohydrates along the essentially leaky sieve cells of the phloem tissue (Christy and Ferrier 1973, Ferrier et al. 1975, Van Bel 1995). We tested the hypothesis that bark water content mainly depends on the amount of total sugars to be transferred. We found a strong positive correlation between the amounts of water and total sugars in all measured spatial and temporal profiles (Figures 4, 6 and 7). However, this finding is not in agreement with the model of phloem water capacitance, because in the model, changing water content leads to changing sugar concentrations (Jarvis 1975). Our findings are consistent with radial transfer of water between xylem and phloem (Figure 15) (Molz et al. 1973), and these radial transfers can be interpreted in relation to phloem transport mechanisms (Lang 1990, Wang et al. 1997).

Temporal profiles at a given stem height showed that sugar concentration and water content varied over time. The translocation of assimilates along the tree stem also shows a diurnal fluctuation because of sugar loading into the phloem. Sucrose and starch accumulate daily in leaves during photosynthetic activity, and sucrose is mainly transferred in the phloem channels during the night (e.g., Hendrix and Huber 1986, Huber et al. 1986). Seasonal changes in starch concentrations in branches and stems have also been reported (Harms and Sauter 1992, Von Fircks and Sennerby-Forsse 1998). The assimilation products move as solute waves down to the stem base at an estimated velocity between 30 and 70 cm h⁻¹ (Milburn 1975). We suggest that the observed temporal variations in amounts of sugar and water at a given stem height (Figures 4a and 4b) are indicative of such waves.

Beside its function as a transport channel, the phloem nourishes the sink tissue around the transport pathway, causing a gradual decrease in solutes toward the stem base (Figure 6) (cf. Minchin and Thorpe 1987). Spatial profiles also confirmed the strong relationship between phloem sugar concentration and phloem water content.

The water capacitance model supposes that relative humidity affects bark thickness as a result of changes in xylem water potential and phloem water content. However, we found that the phloem water content did not track changes in either relative humidity or bark thickness (Figures 8–10), which relates xylem water potential to a secondary role among the driving forces determining phloem water content. Holbrook (1995) argued that the high differentiation of the cells in this region makes it unlikely that they are also responsible for the hydration of other parts of the plant.

Changes in bark thickness closely followed changes in relative air humidity, but with a lag of 2 to 3 h (Figures 8–10).

**Table 1.** Volume and weight changes (SE in parenthesis) of isolated bark cores after different treatments. Calculated values are given as percentages based on fresh weight and fresh volume determined immediately after collection (n = 10).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Cortex</th>
<th></th>
<th></th>
<th>Nonconductive phloem</th>
<th></th>
<th></th>
<th>Conductive phloem</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Δ Volume</td>
<td>Δ Mass</td>
<td></td>
<td>Δ Volume</td>
<td>Δ Mass</td>
<td></td>
<td>Δ Volume</td>
<td>Δ Mass</td>
</tr>
<tr>
<td>After degassing</td>
<td>+5.8</td>
<td>+59.0</td>
<td>(2.1)</td>
<td>+0.6</td>
<td>+47.7</td>
<td>(12.3)</td>
<td>+0.05</td>
<td>+35.9</td>
</tr>
<tr>
<td>Watering for 3 h</td>
<td>+15.6</td>
<td>+88.7</td>
<td>(3.4)</td>
<td>+8.2</td>
<td>+67.8</td>
<td>(13.2)</td>
<td>+2.6</td>
<td>+35.9</td>
</tr>
<tr>
<td>Total dry out</td>
<td>−14.7</td>
<td>−11.0</td>
<td>(4.0)</td>
<td>−21.4</td>
<td>−26.2</td>
<td>(2.4)</td>
<td>−45.0</td>
<td>−59.2</td>
</tr>
<tr>
<td>Re-watering for 48 h</td>
<td>+7.6</td>
<td>+100.3</td>
<td>(3.4)</td>
<td>+4.2</td>
<td>+70.4</td>
<td>(11.6)</td>
<td>−18.8</td>
<td>+4.3</td>
</tr>
</tbody>
</table>

Figure 14. Temporal changes in (a) bark thickness, (b) thickness of boiled phloem and (c) cortical thickness (thick line) of small bark chips together with relative air humidity (thin line). Dendrometer recordings were made on small bark chips (1 cm²) glued to a metal plate and maintained in a climate chamber at a constant temperature of 20 °C.
Controlled changes in relative humidity also induced corresponding changes in the thickness of isolated bark chips glued to a metal plate (Figure 14), indicating that relative humidity provides a driving force sufficient to explain changes in bark thickness under temperate conditions \((T_{\text{air}} > 0 ^\circ \text{C})\). The relationship between xylem sap velocity and changes in bark thickness breaks down not only in the climate chamber, but also under specific field conditions; for example, when stomatal closure prevents transpiration. The absence of a relationship between bark thickness and xylem sap velocity in living tree stems was noted on several occasions in winter \((T_{\text{air}} > 0 ^\circ \text{C}, \text{Figure 13})\) and on one summer night (Figure 11). These results confirm the findings of Lövdahl and Odin (1992), who suggested that changes in bark thickness under moderate conditions are mainly driven by changes in relative humidity. However, there is also a direct effect of air temperature on stem thickness as exemplified by the frost-induced changes shown in Figure 12 (cf. Loris et al. 1999, Zweifel and Häslér 2000).

Herzog et al. (1995) considered that the hygroscopic properties of tree bark may affect dendrometric measurements but postulated that hygroscopicity is restricted to the dead layer of the bark. This is not the case however, because the phloem tissue also responds to such changes (Figure 14). Moreover, we observed changes in bark thickness in intact as well as in boiled tissues, demonstrating that dead cells can produce changes in bark thickness. These findings indicate that swelling and shrinking of the cell walls is the underlying phenomenon, rather than turgor changes. Swelling and shrinking of cell walls is probably associated with their high contents of hydrophilic compounds, such as pectin or hemicellulose (Frey-Wysling 1976).

It is generally assumed that the reversible changes in bark thickness are primarily a result of water exchanges between xylem and phloem driven by changes in xylem water potential as a result of changes in transpiration rate (Dobbs and Scott 1971, Jarvis 1975, Herzog et al. 1995). This assumption is based on synchronous measurements of xylem flow activity and changes in bark thickness. However, transpiration and the hygroscopic response of the bark are mainly driven by VPD and relative humidity, respectively, which are correlated under moderate field conditions; therefore, it must be expected that they frequently show the same temporal patterns. We hypothesize that the correlation between xylem water potential and transpiration on the one hand and changes in bark thickness on the other hand is circumstantial rather than causal.

We observed a lag of 2 to 3 h between changes in xylem flow activity and changes in bark thickness (Parlange et al. 1975, Milne et al. 1983, Herzog et al. 1995). A similar lag was observed between changes in relative air humidity and changes in bark thickness, indicating that transpiration was not responsible for the lag (Figure 14). Relative humidity is a more relevant parameter than VPD (cf. Oren et al. 1999) when considering processes underlying changes in bark thickness, because water exchange between the stem surface and the atmosphere is a two-way process between two water-unsaturated media.

Except for small hygroscopic effects, we found that changes in phloem water content had no effect on bark thickness, suggesting that sufficient intercellular airspace exists. The bark of Norway spruce contains large areas with crushed and dead sieve cells (Figure 16) that could compensate for volume.

Figure 15. Diagrammatic representation of water circulation and phloem transport in higher plants. Permanent and intense release and retrieval processes along the conductive phloem are accompanied by the continuous exchange of water, which is probably withdrawn from the xylem, as indicated in the diagram. Solutes are diluted toward the stem base as a result of essential biochemical processes, such as respiration, growth and storage. Abbreviation: suc = sucrose.

Figure 16. Cross section of a stem segment of P. abies. White arrows indicate the crushed and dead sieve cell zone.
changes of the living phloem cells or even generate volume changes themselves by swelling and shrinking, independently of the total water content of the living tissues. This was also suggested by Holbrook (1995) with reference to the parenchymatous matrix of monocotyledons. We found that up to 24% of the volume of isolated phloem cores was air-filled space, which can accommodate more than the full range of observed changes in water content.

A direct relationship between thickness changes and xylem flow activity may exist in other plants or plant compartments. For instance, McBurney and Costigan (1984) found no time shift between changes in xylem water potential and changes in stem thickness in young cabbage plants. Irvine and Grace (1997) and Offenthaler et al. (2001) reported large changes in thickness based on measurements of the woody cylinder of mature Pinus resinosa Ait. and Picea abies, respectively, but no time lag between changes in thickness and changes in xylem water potential was found in either study. Previous studies have reported thickness changes of the woody cylinder as negligible (Dobbs and Scott 1971, Molz and Klepper 1973, Siau 1984). However, these findings are not directly comparable with results obtained from whole tree stems including the bark. Therefore, we conclude that measurements of bark thickness changes in Norway spruce stems are not indicative of changes in either xylem flow activity or phloem water capacitance.

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