Climatic drivers of hourly to yearly tree radius variations along a 6°C natural warming gradient

Greg King1,2*, Patrick Fonti1, Daniel Nievergelt1, Ulf Büntgen1,2, David Frank1,2

1 Swiss Federal Research Institute WSL, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland
2 Oeschger Centre for Climate Change Research, Zähringerstrasse 25, 3012 Bern, Switzerland

*Corresponding author: e-mail: gregory.king@wsl.ch; phone: +41. (0)44.739.2816

Additional author e-mails:

patrick.fonti@wsl.ch; david.frank@wsl.ch; ulf.buentgen@wsl.ch; daniel.nievergelt@wsl.ch

Submission to Agricultural and Forest Meteorology

Mar 28, 2012
Abstract

Climate influences the timing, rate and dynamics of tree growth from sub-hourly to multi-centennial timescales. Monitoring of stem radius variations on the temporal scales at which many physiological processes operate is necessary to obtain insight into intra-annual stem dynamics and contribute to the understanding of climate impacts on growth processes. Here, we quantify the response of radial conifer stem size to environmental fluctuations via a novel assessment of tree circadian cycles from four years of sub-hourly data collected from 56 larch and spruce trees growing along a natural temperature gradient of ~6°C located in the central Swiss Alps. During the growing season tree stem diameters were greatest at mid-morning and smallest in the late evening, reflecting the balance of transpiratory water loss and uptake from the roots. Along the gradient, amplitudes calculated from the stem radius cycle were ~50% smaller at the upper site (~2200 m a.s.l.) relative to the lower site (~800 m a.s.l.). We show that typical growing season diurnal cycles are substantially modified by changes in precipitation, temperature and cloudiness; amplitudes were nine times smaller on days with rain (>10 mm) and daily amplitudes increase by ~40% if mean daily temperature is between 15-20°C compared to 5-10°C. We find that over the growing season in the sub-alpine forests, spruce show greater daily stem water movement than larch. However, under projected future warming, larch could experience up to 50% greater stem water-use, which on already dry sites may severely affect future growth. Our data further indicate that the confounding influences of radial growth and short-term water dynamics on stem size likely lead to an overstated importance of water-linked meteorological variables on intra-annual tree growth using conventional methodology. We suggest that intra-seasonal measurements of cellular development and consideration of reversible changes in stem diameter due to climatic factors will be necessary to reduce possible biases in quantifying and attributing changes in forest productivity in response to future warming.
Introduction

Trees play a key role in the dynamics and coupling of the carbon and hydrological cycles (Hutjes et al., 1998; Prentice et al., 2000). In forested regions, approximately half of the precipitation is returned to the atmosphere through tree stems (Oki and Kanae, 2006). In parallel, tree photosynthetic activity constitutes approximately 50% of the total terrestrial net primary production (Bonan, 2008). These characteristics, together with additional ecosystem services, make the quantification of tree growth and its environmental interactions an important task, especially under continuing global change (IPCC, 2007).

Atmosphere-landscape feedbacks are an example of important regional to global phenomena well addressed by large-scale data sets and modelling approaches (Seneviratne et al., 2006; Frank et al., 2010; Jung et al., 2010), although tree-based measurements are still necessary to monitor and attribute growth. Repeated observations (e.g., tree diameter and height) are commonly employed to track biomass accumulation (Husch et al., 2003), whereas increment cores provide retrospective quantification of annual radial growth (Fritts, 1976). These methods offer the basis to statistically link inter-annual to long-term growth with, at best, monthly climatic variables. To improve our understanding of the physiological mechanisms driving tree growth, sub-daily and cellular scale data are required.

Dendrometers meet these conditions by recording stem radius at sub-hourly and micrometer resolution (Daubenmire, 1945; Bormann and Kozlowski, 1962; Drew and Downes, 2009), with observed variations representing a combination of growth together with water transport and storage...
Automatic dendrometers are now widely used to provide data on coniferous and broadleaf trees from boreal to tropical forests (Perez et al., 2009; Biondi and Hartsough, 2010; Nabeshima et al., 2010; Oberhuber and Gruber, 2010; Duchesne and Houle, 2011). For example, dendrometers have been used to quantify and date the seasonal progress of wood formation, providing the basis for intra-annual tracing of isotope (e.g. $\delta^{13}$C and $\delta^{18}$O) signatures from source to sink for an entire growing season (Gessler et al., 2009; Offermann et al., 2011). However, most studies have focused on isolating tree growth, typically via the so-called “daily” (Tardif et al., 2001; Bouriaud et al., 2005), or “stem cycle” (Downes et al., 1999; Deslauriers et al., 2003) approaches, to explore the influence of environmental variables. Over three years Deslauriers et al. (2003) attributed daily radial growth of balsam fir (Abies balsamea (L.) Mill.) in the boreal forest primarily to water availability and demands. Similarly, daily radial changes of tree species from Ecuador and Ethiopia measured with dendrometers were explained by available moisture with the vapour pressure deficit and precipitation being the most important factors (Bräuning et al., 2009; Krepkowski et al., 2011). The daily increment of Pinus cembra (L.) at the alpine ecotone (Gruber et al., 2009) has also been positively correlated with changes in tree water status (relative humidity and precipitation). Less emphasis has been placed on the stem water signal and how it actually may confound the attribution of growth (Zweifel et al., 2001; Makinen et al., 2003). Consequently, investigations focusing on tree water balance will contribute to improving the isolation of the growth signal, quantifying processes such as transpiration rates and water-use efficiency, and increasing understanding of soil-plant-atmosphere coupling.

Here, we present high-resolution stem radius measurements collected over four years (2007-2010). We use a novel data analysis approach to i) isolate diurnal cycles, ii) examine the stem water signal and iii) attribute the influence of environmental drivers. These analyses are examined in two
different common alpine species: Norway spruce (*Picea abies* Karst.) and European larch (*Larix decidua* Mill.), along a temperature gradient over a complete year. To this end, sub-hourly stem radius measurements from 56 trees at eight sites along a 1400 m altitudinal gradient were collected with associated instrumental data. The altitudinal transects provide a ~6°C growing season temperature difference, roughly corresponding to the projected increase of Switzerland summer temperatures to the year 2100 under scenario A1B (CH2011, 2011) and allowing us to make inferences as to the impacts of a warming climate.
Material and Methods

2.1. Study Area

Our study was conducted across two altitudinal transects centered in the Lötschental (46°23′40″N, 7°45′35″E), an inner-alpine valley located in the central Swiss Alps (Fig. 1a). The valley is enclosed by steep forested slopes (mostly >60%) primarily composed of mixed, evergreen Norway spruce and deciduous European larch extending to ~2300 m a.s.l. The soils along the transect are acidic and characterized by a large stone content and low amounts of clay. Different soil types were observed, ranging from Leptosol, Cambisol to Podzol, with intermediates (IUSS Working Group WRB, 2006). The soils were formed from calcareous-free parent material, including moraines and crystalline bedrock (gneiss and granite) from the Aar massif (Jemelin et al., 1985). The region has a cool climate with a mean annual temperature of 5.7°C, ranging from -3.3°C (January) to 14.8°C (July). As a relatively dry region, the mean annual precipitation is 825 mm and is well distributed throughout the year with precipitation falling predominantly as snow between November and March (MeteoSwiss sites, Fig. 1a). During the study (2007-2010) conditions were broadly similar to the long-term average (1987-2006) except for a slightly warmer spring (attributable to a very warm 2007) and more precipitation received over the late spring and summer and less in the early autumn (Fig. 2).

Measurements were performed at eight sites (Fig. 1). Seven sites were established at 300 m elevation intervals starting from the valley bottom, located at ~1300 m a.s.l., along both the northwest and southeast slope aspects until ~2200 m a.s.l., just below the upper forest limit. To further extend the altitudinal gradient, an additional site was established in early 2008 just outside of the Lötschental in the main Rhône valley on a north-facing slope at an elevation of ~800 m a.s.l. Codes for aspect and altitude (in hundreds of meters) were assigned to each site (e.g. N13 or S22). Site temperatures decline by 0.47 °C/100m on the south- and 0.42 °C/100 m on the north-facing slope and between-slope differences were generally absent.
2.2. Data Collection

2.2.1. Dendrometers

At each site, with the exception of N22 and S22 which are above the local altitudinal range of spruce, four mature, dominant and healthy trees of each species (*Picea abies* and *Larix decidua*) were selected for a total of 56 trees. The sampled trees have average heights of 27 m and diameters of 44 cm, and were similar for both species. Trees located along the two transects are generally older at higher elevations (e.g., average of 251 years at 2200 m a.s.l. and 116 at N13), with larch and spruce exhibiting similar ages at the same site (Bechet, 2010). Automatic dendrometers were installed on all trees to continuously measure stem radius changes (DR, *Difference in Radius over time*). Two different dendrometer types were equally distributed among species and sites: a point dendrometer and a circumference dendrometer, models DR and DC-1, respectively (Ecomatik, Munich, Germany). The measurement of stem radius requires the conversion of a distance change in the sensor rod for the point dendrometers (band length for the circumference dendrometers) into an electrical signal using a linear variable differential transformer. Signals were corrected for thermal sensitivity according to the manufacturer’s specifications.

Data were recorded from October 2006 to October 2010 with a sampling resolution of hourly or better. The resulting data were processed to identify and correct errors due to factors such as animals eating wires, moisture entering the data logger housing, fallen trees, and on one occasion an errant (or precisely placed) hunting bullet. In addition, tension on the dendrometer sensor rods and wire bands was periodically adjusted to remain within the manufacturer’s measurement range as the trees grew. Gaps (which remained unfilled) and abrupt jumps were corrected considering series from neighboring trees without the corresponding inhomogeneity. Sub-hourly DR values were averaged to hourly resolution. To investigate diurnal cycles, the overall growth trend was removed from the data by calculating daily means for each sensor and subtracting it from the measurements.
2.2.2. Meteorological Measurements

Site conditions were continuously monitored using a variety of sensors. From 2006 onwards stem temperatures at each site were measured every 15 minutes with a temperature logger (Onset, Tidbit) installed on a single tree at about 1.6 m above the ground and protected from direct solar radiation. Starting in the spring of 2008, air temperature, relative humidity (RH) and dew point were recorded at 15 min resolution using a sensor (Onset, U23 Pro) placed beneath the canopy at each site. Furthermore, temperature, precipitation and radiation records were compiled using a network of MeteoSwiss sites in the region (Fig. 1a). This network was selected based on multiple comparisons including those with a temporary meteorological station installed in the Lötschental near the village of Wiler. This network provided a historical baseline (1987-2006) of hourly precipitation and temperature observations for our study.

2.3. Data Analysis

To explore the characteristic diurnal cycle of DR, which resembles a sinusoid waveform, we define several metrics based on characteristic data patterns (Fig. 3). The local maximum \( (R_{\text{max}}) \) and minimum \( (R_{\text{min}}) \) are found at the critical points of the wave. From these points, the timing of the daily maximum \( (T_{\text{max}}) \) and minimum \( (T_{\text{min}}) \) were calculated, as well as the peak-to-peak amplitude \( (\Delta R = R_{\text{max}} - R_{\text{min}}) \). On rare days when stem size increased monotonically, no values were assigned.

To investigate the influence of air temperature on diurnal amplitude over the growing season we averaged observations over all years and used site as our unit of replication \( (n = 8) \). As we are interested in a general response across all elevations, a linear mixed-effects model (R package lme4) was fit to the data considering air temperature as a fixed effect and site as a random effect. To compare species response we fit larch and spruce independent of each other. As there is no consensus as to the best method for calculating an R2 for this type of regression, we instead
calculate the correlation between observed and predicted values (Byrnes et al., 2006) for an intuitive measure of how well our proposed model explains observed variation in the data.

To further explore circadian cycle shifts during the growing season, we classified and averaged daily changes in stem size according to meteorological conditions as reported in the regional network. We calculated different classes for daily precipitation, temperature, sunshine percentage as well as a weather index combining precipitation and sunshine amounts. Each of these variables was selected based upon previous research that identified their importance for tree transpiration processes (Jarvis and McNaughton, 1986).

All analyses were performed using the R statistical environment (R Development Core Team, 2012).
3. Results

3.1. Stem radius variations

From 2007-2010, the stem radius variations (DR) showed annual and daily cycles characteristic of trees growing in temperate regions (Fig. 4). Trees generally reveal a synchronous response, although more coherence is found at the site-level than across the altitudinal transect. The annual variability is characterized by a progressive increase of stem radius beginning in the spring, a plateau in late summer and a decrease during the winter months (Fig. 4a and 4c). The stem radius increase is closely linked with the main period of xylogenesis. The subsequent plateau in stem size suggests a reduction in cellular division and expansion, while the winter decrease indicates stem desiccation. At our sites, the amplitude of this seasonal cycle is in the range of several thousand micrometers. Within these annual cycles we also observe more abrupt stem size variations in both larch and spruce, usually on the order of hundreds of micrometers. Decreases during the wintertime are related to freezing events, while increases during the growing season are associated with precipitation. At higher resolution during the growing season (Fig. 4b and d), the DR variations show a clear diurnal cycle that appears to be primarily elastic. Obscuration of this daily cycle by stem expansion during precipitation events is readily visible. The daily amplitude during the growing season is about 100 μm (0.1 mm). Figure 5 provides a close-up of the stem contraction events from December 2009 and shows their relation to site-specific air temperatures below -5°C (shaded in red). During this period, the “threshold” temperature is reached at all sites around December 14 and remains low for between 5 and 7 days, with much colder temperatures, a longer duration and larger stem contractions at higher elevations (e.g. S19 drops below -15°C and has a stem contraction of about 2000 μm). Stem size at N08 (the lowest elevation) recovers more quickly and does not record the subsequent temperature decrease and corresponding stem contraction around 28 December.
Comparisons of monthly mean diurnal cycles over a full year reveal variation with the seasons and with site elevation (Fig. 5 and Table 1). The amplitude and phase of the cycles were found to vary along the course of 12 months with notable differentiation between summer and winter. The summer and winter patterns contain a local amplitude maximum in July (99.8 ± 31.4 μm) and February (30.5 ± 18.0 μm), respectively, with the amplitudes being much larger during the summer than the winter. The summer and winter patterns are most characteristically differentiated by a phase shift in the diurnal cycle. During the summer, a local maximum occurs between 0700 and 0900 Central European Time (CET; i.e., between the 8th and 10th hours of the day) followed by a local minimum between 1700 and 2000 CET. Conversely, in the winter the maximum is found between 1700 and 1900 CET, while the local minimum occurs between 0900 and 1100 CET. In addition to the seasonal influence, the characteristics of the daily cycle also change along the altitudinal gradient. As site elevation decreases from 2200 m (orange line) to 800 m (red line) a parallel increase in amplitude is observed, consistent with the observation of the greatest amplitudes during the warmest months. Similarly, as elevation increases, the phase shift in the diurnal cycles from the winter to summer pattern takes place at a later date. These observations of the diurnal amplitude and phase and their modulation with site elevation and the seasonal progression suggest that these characteristics are driven by climatic controls and also provide insight about water movement and storage in trees.

Air temperature is the primary environmental factor that changes with seasons and along the gradient. To investigate its influence on daily cycle amplitudes we plotted monthly mean amplitudes against mean monthly temperatures (April to October) for each site (Fig. 6). The linear mixed effects model revealed a positively correlated increase in the amplitude of the diurnal cycle with increased air temperatures for both species (Larch: $R^2_{\text{COR}} = 0.868$, d.f. = 56; Spruce: $R^2_{\text{COR}} = 0.766$, d.f. = 40). Each species had very different intercept values (55.88 and 6.804 μm, for spruce and larch respectively), indicating that within the current temperature range, spruce experience
larger peak-to-peak amplitudes than larch (e.g. at a temperature of 10°C, expected amplitude of spruce is 118.4 μm, whereas larch is 94.4 μm). The slopes of the species regressions were also different (6.252 μm for spruce and 6.804 μm for larch), which under projected scenarios of warming replicated by the altitudinal gradient would mean an approximate 48% increase in amplitude for an average larch (compared to a 30% increase for spruce) during the month of June.

3.2. Climatic influence on diurnal stem cycles

To obtain further insights as to the influence of climatic factors on the diurnal cycle during the growing season (April-October), data were classified according to levels of precipitation, temperature and sunshine (Fig. 7 and Table 2). Amplitude of the daily cycle was inversely related to precipitation amounts (Fig. 7a). During the growing season, days without precipitation reveal mean amplitudes of 95.8 ± 34.5 μm, compared to 10.6 ± 4.5 μm on days with >10 mm of precipitation. The time of the local maximum stem radius (R_{max}) on these days was also delayed by about two hours (8.14 ± 0.2 to 10.25 ± 0.3 hours). Increases in stem radius over a full day were generally observed starting with the 1-5 mm precipitation category, with a tendency toward monotonic increases in stem size during larger precipitation events. Conversely, an increase in the daily cycle amplitude is observed with a higher average daily temperature (Fig. 7b). Days with a mean temperature from 5 to 10°C show daily amplitudes about 40% smaller than days with mean temperatures between 15 and 20°C. Despite days with higher temperature leading to general decreases in stem radius, no monotonic decreases were observed. Similarly, a greater amount of sunshine results in a greater amplitude of the diurnal cycle (Fig. 7c). On cloudy days (0 – 20% sunshine) the average amplitude is 11.4 ± 8.6 μm, compared with sunny days (> 60% sunshine) when the average amplitude is 106.2 ± 35.2 μm. Additionally, T_{max} occurs about 4 hours earlier in the day as the sunshine percentage increases from 0% to >60%. These amplitude increases suggest
a depletion of stem water reserves in response to greater evaporative demand driven by warmer temperatures and increased sunshine.

While the data show a clear response of diurnal cycles to climatic variables, attributing this response is challenged by the correlation among parameters (e.g., sunny days also tend to be warm days). To help address this, we calculated average daily cycles for a weather index grouping days according to combined radiation (i.e., greater than or less than 40% sunshine) and presence of precipitation (Fig. 7d). The amplitudes during sunny days are minimally affected by the presence (104.6 ± 30.8 μm) or absence (100.0 ± 33.8 μm) of rain. However, cloudy days (independent of precipitation) have about 50% lower amplitude than sunny days and large differences in amplitude with (28.9 ± 14.2 μm) or without (72.4 ± 27.3 μm) precipitation. These patterns suggest that radiation has a greater influence on the diurnal cycles than precipitation, whose influence is moderated by the amount of radiation. These results support the observation that transient atmospheric conditions are coupled with daily water movement within tree stems.

In addition to the responses due to short-term atmosphere-tree coupling, the diurnal cycle characteristics can also supply information about plant responses to the more slowly changing soil conditions. In the Lötschental, soil water reserves during the growing season are primarily recharged by precipitation; we therefore investigate diurnal cycle modulation as a function of the time since the last rain event (Fig. 8). As the length of the rain-free period increases, a clear tendency for decreasing amplitude is observed in both species, although overall, spruce show a 40% greater average amplitude of the diurnal cycle (96.7 ± 18.8 μm) compared with larch (57.6 ± 15.2 μm). Our data appear to reveal species-specific responses to short-term water stress, with spruce maintaining similar daily amplitudes up to 5-6 days following the last rain event before a precipitous 40% decrease of amplitude after 9-10 days. Larch shows a more constant decline in amplitude over time. Although larch has a greater decrease of its amplitude fraction (50% after 9-10 days) than spruce, they do not show any sudden decreases of stem water movement. These
observations lead us to infer that the monitored species have different physiological mechanisms for dealing with short-term water stress.
4. Discussion and Conclusions

4.1. Mechanisms

Our high-resolution measurements collected over four years allow us to improve our physiological understanding of diurnal cycle mechanisms: transpiration and water uptake during the growing season and winter freeze-thaw. Both mechanisms are fundamentally linked with water movement and storage in the elastic stem tissues (Zweifel et al., 2001).

During the growing season, the daily cycles (Fig. 3) reflect a delicate balance between canopy water loss and soil water absorption (Wronski et al., 1985; Kozlowski et al., 1997; Devine and Harrington, 2011). We observed stem contraction generally from mid-morning until early evening when canopy water demand exceeds water absorption via the roots (Herzog et al., 1995; Kozlowski et al., 1997). Conversely, expansion of the stem, when water uptake is greater than losses to the atmosphere (Kozlowski and Winget, 1964), starts in the evening and continues to the following morning. Absorption by the root system occurs more slowly than water losses from transpiration resulting in a more negative water potential within the sapwood (Herzog et al., 1998).

This decreased potential initiates a transfer of water from surrounding elastic tissues (e.g., enlarging xylem cells, cambial cells, phloem, and bark parenchyma) towards the xylem resulting in a decrease of stem size (Zweifel et al., 2000; Zweifel and Häsl, 2001; Sevanto et al., 2011). Beginning in the evening, the water potential in the xylem increases as the stem is refilled by the uptake of soil water. These changes in stem size, quantified by the amplitude in our study, are signals integrating physiological responses to environmental variability. The timing and magnitude of daily stem contractions provide insights as to the relative changes in transpiration and/or soil water status over time.

In comparison to the growing season, during winter, a phase shift in the daily cycles is observed with maximum stem size in the late afternoon (Fig. 5). In our study, the similarity of stem size changes between deciduous larch and evergreen spruce (not shown) demonstrates that
transpiration is no longer the primary driver of winter circadian stem cycles. These observations agree with Sevanto et al. (2006), who studied stem diameter variation of Scots pine in southern Finland, and concluded that although photosynthesis was observed during the winter, air temperature is the dominant factor determining stem size fluctuations. The winter cycles have been attributed to osmotic water movement due to temperature changes around the freezing point of the sap (Zweifel and Hasler, 2000; Mayr et al., 2006). When temperatures sink below approximately -5°C, extra-cellular water begins to freeze inducing the osmotic withdrawal of intra-cellular water and thus cell and ultimately stem shrinkage (Zweifel et al., 2000; Pearce, 2001; Strimbeck et al., 2008). When temperatures rise sufficiently during the day the process is reversed and water begins to flow back into the cells, leading to stem expansion and a daily maximum (Turcotte et al., 2009). The daily amplitudes that result from these freeze-thaw processes are much smaller than the transpiration driven signals observed during the growing season. However, the same physiological process can result in sudden large decreases in stem size, as exemplified in Figure 5, which correspond to events of sudden, large temperature decreases below the freezing point of sap. We hypothesize that a sudden temperature decrease results in larger stem size reductions because a greater volume of water is frozen. Additional evidence for temperature as the driver of these winter freeze-thaw cycles from our study is the relative absence of freeze-thaw events at N08, the warmest site on the altitudinal transect. A comparison of the air temperatures between N08 and all other sites reveal a difference of ~5°C during the winter, large enough that temperatures rarely descend below the sap-freezing point. Additionally, the mean daily cycle at N08 does not show a clear phase shift during the winter months concurrent with the other seven sites. We conclude that there is a distinct winter diurnal cycle and that is driven by ambient temperature changes. Although not occurring during the growing season, the diurnal cycles captured by dendrometers represent an opportunity to further investigate the impact of freezing and thawing on tree growth.
4.2. Variation of daily cycles over seasons, elevation and between species

The magnitude and duration of annual cycles from our sites are within the range of those described from other gymnosperms at both alpine and boreal locations (Tardif et al., 2001; Zweifel and Häslер, 2001; Biondi et al., 2005; Duchesne and Houle, 2011). Our observation of phase shifts of the diurnal cycle when comparing cycles in both winter and summer broadly agrees with Turcotte et al. (2009), who divide the year into three periods: winter shrinkage, spring rehydration and summer transpiration based on the timing of daily stem contraction and expansion as well as the temperature during these phases. However, we did not consistently identify a true spring rehydration period, defined as the period when plant tissues rehydrate in preparation for cell division (Turcotte et al., 2011). Instead, our observation of low diurnal amplitudes in March is a function of the shift between winter and summer and the destructive interference between their respective waveforms, which are either temperature driven or a function of active water movement in the stem. This conclusion is supported by the amplitude minimum observed in November at the end of the growing season and start of winter dominated cycles.

Our study is unique in its ability to assess how seasonal transitions take place across an altitudinal transect, providing a natural ecological experiment with a steep environmental gradient driven by temperature (Körner, 2007). We observe that summer diurnal cycles occur earlier at sites located at lower elevations and similarly, the transition to winter cycles takes place later in the autumn. Based upon our altitudinal gradient, we propose that the primary factor driving transitions between cycles is temperature. Temperature thresholds for the beginning of xylogenesis and more general vegetative biological activity are suggested to occur when daily temperatures exceed 4-6°C (Körner, 2006; Rossi et al., 2008). Sites located at higher elevations (1900 and 2200 m a.s.l.) require more time to surpass these temperatures, inferring that summer diurnal cycles of trees at these locations would start later than trees at 1300 or 800 m a.s.l. This conclusion is supported by the work of Moser et al. (2010), who investigated the timing of xylem formation in Larix decidua
across this altitudinal gradient during the 2007 growing season. They found that needle budburst
and each phase of xylogenesis started later at higher elevations (2.9 - 3.7 days/100 m). These delays
were associated with temperature declines as altitude increased and a lengthening of the overall
growing season of ~7 days/°C, suggesting that temperature is the primary control for growth onset.

Investigations of the relation between air temperature and daily cycle amplitude at our sites
showed clear increases of amplitude with increased temperature, which we relate to increased
canopy transpiration rates and water demands. Comparison of the diurnal cycles and regression
equations for the monitored species (Picea abies and Larix decidua) reveals similar timing for the
beginning of stem water use, but greater amplitudes in spruce. This implies that during a diurnal
period, Picea abies exploit their internal stem water reserves more quickly than Larix decidua. One
possible explanation for this pattern is that European larch have a greater conductivity area and
therefore a greater capacity for water reserves compared to Norway spruce (Schulze et al., 1985;
Gower and Richards, 1990; Bryukhanova and Fonti, in review). An alternative and perhaps more
simple hypothesis relates to the difference in the root systems between the two species. As a pioneer
species, larch have deeper root systems than spruce and this may allow larch to access additional
soil water resources and limit the use of internal reserves (Gower and Richards, 1990; Tjoelker et
al., 2007). However, with projected warming, we expect larch will experience greater stem
contraction with increasing temperatures and at the warmest sites, perhaps eventually exceed the
daily amplitude of spruce. These results are in agreement with recent research from lower-elevation
sites in the Swiss Alps that has found European larch growth had the most-negative response to
soil-water limitations (Eilmann and Rigling, 2012). These high rates of water-loss on already dry
sites could severely limit growth and may even lead to tree death.

4.3. Climatic drivers
In addition to examining the spatial and temporal aspects of the diurnal stem cycle, we also investigated the influence of different meteorological variables on circadian rhythms. Similar to our findings, investigations performed with high-resolution measurements of stem size consistently find responses to changes in the short-term weather conditions (Fritts and Fritts, 1955; Kozlowski and Winget, 1964; Herzog et al., 1995; Devine and Harrington, 2011). However, with our methods, we are also able to examine daily stem size variations on an annual scale and find that maximum amplitudes of the daily cycles were found in June and July, coinciding with the highest temperatures at the study sites. Additionally, intensification of the daily amplitude was found with increasing daily mean air temperatures and greater amounts of sunshine. Both of these variables act to increase the amount and rate of daily transpiration (Jarvis and McNaughton, 1986; McKenney and Rosenberg, 1993). Increased transpiration leads to elevated water demand and due to time lags with the root system, individuals must fulfill any difference in water requirements with water stored in internal tissues (Herzog et al., 1998; Zweifel and Häsl, 2001). If trees do not utilize stem water, it may be necessary to close stomata, which can result in carbon starvation and negative consequences for tree growth (McDowell et al., 2008; Eilmann et al., 2009).

We see indications of these patterns when evaluating species diurnal cycle response to periods without rain. Spruce experiences similar stem cycle amplitudes for approximately six days before undergoing a large decrease of stem size oscillations. This behavior is consistent with a more negative xylem water potential and stomatal closure to prevent large water losses when soil reserves are incapable of fully replacing stem water. In contrast, larch experiences a slow, steady amplitude decline indicative of greater water use to buffer increased demand. These results agree with observations from the European Alps, which found that trees reduce their rates of transpiration slowly with decreasing availability of water resources from the soil, and only show large reductions in water use after specific thresholds are exceeded (Anfodillo et al., 1998; Clausnitzer et al., 2011).
These observations indicate that the internal storage of water and the mobilization of these sources on a daily basis are essential to tree productivity.

Our data also indicate that days with more precipitation were shown to have smaller and delayed stem contractions. Precipitation events lead to an increase in available soil water, but there is also evidence that rain intercepted by needles and branches can be directly absorbed and used for transpiration demands from the canopy (Katz et al., 1989). However, the delay of stem contraction observed on rainy days may also suggest that instead of changing water sources, the internal reserves of the tree are still utilized, but are refilled nearly at depletion rate (Zweifel and Häsler, 2001; Steppe et al., 2006; Deslauriers et al., 2007). Regardless of the path, availability of water from alternative sources reduces demand on internal water reservoirs. In addition, our weather index revealed that the amount of sunshine moderated the influence of precipitation on the daily stem amplitude. Increased radiation results in greater transpiration rates, leading to increased stem water mobilization and thus greater stem contraction (increased amplitude). These conditions appear to counteract any reduction of stem contraction based on the presence of precipitation.

However, during cloudy conditions and presumably decreased transpiration rates, increased water availability from precipitation has a clear offset on the amount of stem contraction.

The plant water system is a continuum between the atmosphere, needles, stems and the soil. Therefore, soil water availability may play a role in modulating the diurnal stem cycle. Kozlowski and Winget (1964) proposed that diurnal stem shrinkage is primarily driven by the depletion of soil water resources. This notion is not supported by our data. Although available soil water certainly plays a role in the dynamics of tree water movement (and specifically short-term water stress), the seasonal course of soil water at our sites decreases over time, from a maximum in spring to a minimum in the fall. These trends do not coincide with the greatest amplitudes at our sites in June and July. A comparison among sites is also unsupportive of the proposal of Kozlowski and Winget (1964). While similar soil water availability exists across the transect (Laubscher, 2009),
temperatures show a definite decrease from highest to lowest elevations, again suggesting reduced stem contraction with increasing altitude is more closely linked to temperatures.

4.4. Implications and Opportunities

As dendrometers are broadly regarded to record tree radial growth, many long-term monitoring programs sites rely upon dendrometer measurements (Jolly et al., 2005). However, it is essential to understand how processes unrelated to growth may bias these estimates. Failing to take into account the variability contained within the annual cycle and intra-seasonal variation in weather and tree water status when deciding upon measurement times and intervals can lead to over or under-estimates of growth. Such biases would have important implications on forest models, land-use management, and carbon accounting schemes.

Dendrometers have also been increasingly used to calculate the growth response to climatic variables. The most common approach for analysis of continuous dendrometer data is the stem-cycle method (Downes et al., 1999; Deslauriers et al., 2003). This method splits the diurnal cycle into phases of expansion, contraction and stem radius increment (SRI) on the basis of calendar days. Once these have been calculated, each phase is commonly correlated with meteorological variables (Deslauriers et al., 2003, 2007; Bräuning et al., 2009; Duchesne and Houle, 2011). Most studies consider the cumulative SRI to be analogous to radial growth and conclude that water based-measures, such as relative humidity and precipitation are the most important factors influencing growth (Oberhuber and Gruber, 2010; Krepkowskiet al., 2011; Volland-Voigt et al., 2011). Our set of methods removes the seasonal growth trend from the dendrometer data, but still reveals a clear increase of stem size on days with precipitation. In the stem-cycle method days with precipitation would be over-represented as days with a positive SRI, resulting in a greater overall contribution to the cumulative SRI. We suggest that this results in artificially inflated importance of moisture related meteorological variables (e.g. precipitation, VPD) during calculation of statistical relations.
Although we acknowledge that turgor is required for cell growth (Verbelen and Vissenberg, 2007), there is no indication that greater amounts of growth take place on days with precipitation, as trees always attempt to maintain turgor through self-regulation of internal movement of water (Kroeger et al., 2011). Our analyses suggest that a clear understanding of possible biases and sources of statistical error are essential to working with dendrometers. Our data indicate that factors such as temperature and radiation play a greater role in fine-scale stem radius dynamics and overall tree growth (as calculated from dendrometer records) than widely acknowledged.

Intra-annual dendrometer measurements are primarily composed of two different signals, water movement within the stem and growth (Herzog et al., 1995). The analyses presented herein have provided a valuable step towards improving our understanding of the factors that influence short-term changes in stem radius and have revealed possible biases in attributing the climatic drivers of radial growth. These novel methods also contributes to the assessment of the relative amounts of transpiration (and photosynthetic activity) between individuals, over time and as a function of climate. Additional investigations linking observations of xylem development to dendrometer records will contribute to quantifying how well irreversible radial growth is also captured. This study has clearly shown strong climatic controls on reversible stem size fluctuations.

Acknowledgements

This work was funded by a Swiss National Science Foundation project (no. 121859) and NCCR Climate (DE-TREE). We thank the WSL Dendro Sciences team for many fruitful discussions, as well as Christian Ginzler for his expertize with GIS, and the residents of Ferden and Kippel, especially Fabian and Ursi Ambord and the local foresters Hans Henzen and Konrad Egger for their support.
Figure Captions:

Figure 1. Study location. (a) Regional map showing the Lötschental (shaded red polygon) and the location of the five MeteoSwiss meteorological stations (red squares) of Evolene-Villa (EVO), Crans-Montana (MVE), Ulrichen (ULR), Visp (VIS) and Zermatt (ZER). (b) Digital elevation model (DEM) of the Lötschental centered around the village of Ferden showing the sampling sites (blue circles); the 800 m a.s.l. site is located just outside the valley is in 1a (blue circle). (c) Schematic diagram of the transect showing site elevations, codes and sampled species.

Figure 2. Comparison of mean daily average temperatures (a), and monthly sums of precipitation (b) for the monitoring years 2007-2010 (blue) and the 1987–2006 average (red). The grey shading in (a) indicates the mean minimum and maximum temperatures averaged over the 1987–2006 period. Data were calculated as an average from a network of five MeteoSwiss weather stations in the region.

Figure 3. A schematic of the diurnal cycle of stem radius (DR). The local maximum (R_{max}) and minimum (R_{min}) stem radius, and the daily amplitude (ΔR), which is difference between the R_{max} and R_{min} are indicated. The T_{max} and T_{min} indicate the respective times when the local maximum and minimum radius occur. A phase shift is represented by the grey dashed line.

Figure 4. Hourly DR records of: (a-b) four trees located at a single site (S16), and (c-d) site averages along a 1400 m altitudinal gradient. The top panels show four complete growing seasons, from 2007 until 2010; and the bottom panels show the same data for a two month period from June 2010 to August 2010.
**Figure 5.** Hourly stem contraction and air temperatures (shaded red below -5°C) from each site along the altitudinal gradient (increasing elevation from left to right). Data are from December 2009 and represents site averages of all tree and dendrometer types.

**Figure 6.** Relations between mean monthly diurnal cycle amplitude and mean monthly air temperature, grouped by species. Regression lines were calculated based on a linear mixed-effects model and were calculated for each species individually. Data are limited to days with no precipitation during the growing season (April-October) over the four growing seasons (2007-2010).

**Figure 7.** Monthly mean circadian cycle during the growing season (April – October) for primary meteorological drivers: (a) the daily amount of rain received; (b) the mean daily temperatures; (c) the amount of sunshine received during a given day adjusted for number of daylight hours; and (d) according to overall weather conditions. Data consist of all point dendrometers averaged across all species and sites and considers four growing seasons (2007-2010). All weather drivers were calculated from the network of five meteorological stations (see Fig. 1).

**Figure 8.** Mean circadian cycles during the growing season (April - October) grouped by the number of days since the last precipitation event. Data is divided by species (a) larch, and (b) spruce. Panel (c) shows the amplitude decrease as time since rain event increases for both species.

**Table 1.**
Descriptive statistics of the monthly mean diurnal cycles presented in Figure 5. Here all five sites are combined to obtain characteristics for each month. Data are composited over four complete growing seasons (2007-2010).

Table 2.

Descriptive statistics of the mean circadian cycle during the growing season (April – October) for primary meteorological drivers as presented in Figure 7. Data consist of all point dendrometers averaged across all species and sites and includes four complete growing seasons (2007-2010).
References:


and Picea trees: A comparison of xylem flow, porometer and cuvette measurements.


Figure 1

- a) Map showing geographical locations labeled with codes.
- b) Detailed aerial view with elevation markers and plant species symbols.
- c) Graph with elevation data and plant species symbols.
Figure 3

- **$R_{\text{max}}$**
- **$R_{\text{min}}$**
- **Amplitude**
- **Phase Shift**

**Daily $\Delta R$ (µm)**

**Hour**

- $T_{\text{max}}$
- $T_{\text{min}}$
Figure 4
Figure 5

![Graph showing mean stem radius (µm) over hours of the day for different months (Jan to Dec) and sites (N08, N13, S16, S19, S22).](image-url)
Figure 6

$y = 6.252 \cdot x + 55.88$

$y = 8.767 \cdot x + 6.804$

Species
- Larch
- Spruce
Figure 7

(a) Daily Mean R (µm)
(b) Temperature (°C)
(c) Sunshine (%)
(d) Weather

- Rain (mm)
  - none
  - >0 to 1
  - >1 to 5
  - >5 to 10
  - >10

- Temperature (°C)
  - >0 to 5
  - >5 to 10
  - >10 to 15
  - >15 to 20
  - >20

- Sunshine (%)
  - 0 to <20
  - 20 to <40
  - 40 to <60
  - >60

- Weather
  - No Rain / Cloudy
  - No Rain / Sunny
  - Rain / Cloudy
  - Rain / Sunny
Figure 8

(a) Mean Daily R (µm) vs. Hour of Day for different Days Without Rain.

(b) Days Without Rain distribution for Larch and Spruce.

(c) Amplitude Fraction for Larch and Spruce.