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Research paper

Temperate tree species show identical response in tree water deficit but different sensitivities in sap flow to summer soil drying

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Temperate forests are expected to be particularly vulnerable to drought and soil drying because they are not adapted to such conditions and perform best in mesic environments. Here we ask (i) how sensitively four common temperate tree species (*Fagus sylvatica*, *Picea abies*, *Acer pseudoplatanus* and *Fraxinus excelsior*) respond in their water relations to summer soil drying and seek to determine (ii) if species-specific responses to summer soil drying are related to the onset of declining water status across the four species. Throughout 2012 and 2013 we determined tree water deficit (TWD) as a proxy for tree water status from recorded stem radius changes and monitored sap flow rates with sensors on 16 mature trees studied in the field at Lägeren, Switzerland. All tree species responded equally in their relative maximum TWD to the onset of declining soil moisture. This implies that the water supply of all tree species was affected by declining soil moisture and that none of the four species was able to fully maintain its water status, e.g., by access to alternative water sources in the soil. In contrast we found strong and highly species-specific responses of sap flow to declining soil moisture with the strongest decline in *P. abies* (92%), followed by *F. sylvatica* (53%) and *A. pseudoplatanus* (48%). *F. excelsior* did not significantly reduce sap flow. We hypothesize the species-specific responses in sap flow to declining soil moisture that occur despite a simultaneous increase in relative TWD in all species reflect how fast these species approach critical levels of their water status, which is most likely influenced by species-specific traits determining the hydraulic properties of the species tree.

Keywords: *Acer pseudoplatanus*, *Fagus sylvatica*, *Fraxinus excelsior*, *Picea abies*, water relations.

Introduction

Climate change is expected to cause changes in precipitation patterns and to increase the frequencies of heat waves and drought events (i.e., below-normal precipitation that lasts for several months to years (Dai 2011)) (IPCC 2013). These climatic changes will have a negative effect on the availability of soil water for trees in temperate forests (Koecher et al. 2009). It has been shown that soil drying can significantly affect the functioning of trees and the delivery of ecosystem goods and services from forests (Ciais et al. 2005, Allen et al. 2010, Reichstein et al. 2013). Understanding the consequences of soil drying for the functioning of trees and forests is thus a key research priority in order to develop sustainable forest management strategies that account for changing climatic conditions and that secure as such the delivery of ecosystem goods and services from forests in the future (Asbjornsen et al. 2011, Klein et al. 2014).

Trees from temperate forests are expected to be particularly vulnerable to soil drying because they are adapted to mesic environments, with typically continuous water availability and absence of seasonal droughts (Ellenberg 1996, Granier et al. 2007). Traditionally, water relations and physiological drought responses of temperate European tree species have been investigated using saplings or small trees, often in artificial settings (Hartmann et al. 2013). More recently, however, researchers have started to investigate the drought sensitivity of mature trees (Lendzion and Leuschner 2008, Zweifel et al. 2009, Meinzer et al. 2013). Mostly these investigations have focused on comparative assessments of sap flow (kg h^{-1}) across different species during naturally occurring soil drying (Holscher et al. 2005, Meinzer et al. 2013, Zapater et al. 2013). Studies conducted during the extreme 2003 summer drought in central Europe found, e.g., a reduction of sap flow by 40% in *Fagus sylvatica*, 50% in *Carpinus betulus* (Leuzinger et al. 2005), and a decrease of 80% in *Picea abies* and *Betula pendula* (Gartner et al. 2009). Similar responses in sap flow were also observed during less intense dry spells. Holscher et al. (2005) found for example a reduction in sap flux density ($cm^3\ cm^{-2}\ h^{-1}$) of 44% in *Tilia cordata*, 39% in *F. sylvatica*, 37% in *Acer pseudoplatanus* and 31% in *C. betulus* at an average vapor pressure deficit (VPD) of 0.9 kPa. Importantly, most studies that have assessed responses of different temperate tree species to soil drying have found that the magnitude of sap flow reduction differed substantially among species. Typically *P. abies*, *F. sylvatica* and *A. pseudoplatanus* have been found to be most sensitive, while *Quercus petraea*, *B. pendula* and *F. excelsior* seem to be more resistant to dry spells and drought that cause a shortage in water supply (Aranda et al. 2005, Gartner et al. 2009, Koecher et al. 2009). Similar patterns have been observed for congeneric species in North America (Meinzer et al. 2013).

The observed species-specific reductions in sap flow occurring in response to soil drying in temperate trees could be the result of intrinsic differences in drought sensitivity, e.g., caused by anatomical and morphological traits that determine the species' hydraulic properties and vulnerability to cavitation in roots, stems and/or leaves (Fritts 1976, Lemoine et al. 2001, Choat et al. 2012). Alternatively, species-specific differences in drought responses have often been explained by species differences in rooting depth and access to different water pools in the soil (Leuzinger et al. 2005, Zapater et al. 2013). Deep-rooting species should experience soil drying later than shallow rooting species, simply because deep rooting trees have access to more persistent soil water supplies. Different drought responses among different species are then simply the result of the tree's access to different water pools (deep vs. shallow) in the soil and a delayed (if at all) impact of the drought event on deep-rooted tree species compared with shallow rooted tree species (Ellsworth and Sternberg 2015).

To date, comparative studies in mature trees that assess the reasons for different drought response of different species are still rare. For such studies, it would be essential to monitor, among others, the water status of the different species at a temporally high resolution in parallel with the physiological drought response (Koecher et al. 2009). When used in comparative assessments across species, these measurements allow evaluating how well a species is supplied with water and to assess as such if different drought responses of different species are simply the result of the tree's access to different water pools (deep vs. shallow) in the soil. Traditionally, tree water status is assessed by measuring pre-dawn and midday leaf water potential using a Scholander pressure bomb (Scholander et al. 1965). While highly informative, the difficulty of this method lies in the restricted access to leaves in the tree canopy of mature trees. An alternative and recently introduced method to determine the water status of trees is to assess the tree water deficit (TWD) (Hinckley and Running 1978, Zweifel et al. 2005). TWD is determined by continuous measurements of stem radius changes using automated dendrometers (Drew and Downes 2009). In general, stem radius changes are driven by two physiological processes: first, stem radius changes due to growth-induced irreversible stem expansion and second, swelling and shrinking of the stem caused by hydration and dehydration mainly of the bark. In particular shrinking of the bark is strongly influenced by the water status of the tree and is typically referred to as TWD (Zweifel 2015). Recent studies have shown that dendrometer based assessments of TWD are tightly correlated to traditionally used measures of tree water status such as foliar water potential measurements (Ehrenberger et al. 2012). The great advantage of TWD is that it can be obtained from automated dendrometer measurements that allow obtaining continuous high resolution assessments of TWD over entire seasons in mature trees whose canopies cannot be easily reached for conventional assessment of tree water status and to precisely monitor as such the onset of drought impacts on mature trees (Zweifel 2015).

For the research presented here, we continuously measured sap flow and fluctuations in stem radius in 2012 and 2013 for four common temperate tree species (*F. sylvatica*, *P. abies, A. pseudoplatanus* and *F. excelsior)* that dominate the canopy of a mixed temperate forest on the Swiss Plateau. The objectives of our work were to (i) determine the effect of naturally occurring soil drying events in a wet (2012) and a dry (2013) year on the tree water status (i.e., the onset of TWD) experienced by the different co-occurring tree species, (ii) assess the sensitivity of sap flow in these four species to soil drying and (iii) evaluate to what extent species-specific responses in sap flow are related to the onset of TWD across four species and determine as such if different drought responses of the investigated species are the result of the tree's access to more persistent soil water supplies.

Materials and methods

Site description

The Lägeren study site is located at the transition from the Swiss Plateau to the Swiss Jura Mountains (47°28′42.0″N, 8°21′51.8″E, 682 m a.s.l.) on a south-facing slope (10°–45°) in the Swiss Jura mountains. The trees in the highly diverse mixed mountain forest are 105–185 years old, with an average tree height of 30 m for the dominant tree species with individuals reaching up to 50 m. The dominant tree species in the overstory is *F. sylvatica* L., with *P. abies*, *F. excelsior*, *Abies alba* Mill. and *A.*

pseudoplatanus L. as companion species (Eugster et al. 2007). The main soil types are rendzic leptosols and haplic cambisols (Heim et al. 2009). Most common bedrocks are limestone and marl that start 0.6–1 m below the soil surface. The climate can be characterized by a mean annual precipitation of 1110–1114 mm (MeteoSwiss stations Dietikon and Otelfingen, respectively) and a mean annual air temperature of 9.4 °C (MeteoSwiss stations Zürich Reckenholz and Zürich, SMA) (reference period: 1981–2010).

Meteorological data

Continuous half-hourly measurements of air temperature and relative humidity (Hygroclip MP400H, Rotronic AG, Basserdorf, Switzerland) were recorded during our study on the top of an eddy covariance tower (47 m height) with data loggers (CR10X and CR1000, Campbell Scientific Inc., Logan, UT, USA). Volumetric soil moisture (Decagon ECH2O EC-20, Pullman, WA, USA) at 0.1, 0.2 and 0.3 m soil depths was recorded with the same logger at 10-min resolution. The National Air Pollution Monitoring Network (NABEL) provided precipitation data measured at 45 m height on the eddy covariance tower at a 10-min resolution. VPD was calculated on the basis of measured relative humidity and air temperature data. As the eddy covariance flux site is operational only since 2004 we used selected meteorological stations to obtain air temperature, VPD and precipitation data for the 30-year reference period 1981–2010. Closest reference stations for precipitation were Dietikon (DIT) and Otelfingen (OTE) and for temperature and VPD Zürich Reckenholz (REH) and the Swiss Meteorological Institute, Zürich (SMA).

Sap flow measurements

We used constant heat flow sensors (SFS2 Typ M, UP Ibbenbüren, Germany) based on the method described by Granier (1985, 1987). One sensor consisted of two copper-constantan-thermocouple needles (20 mm length), of which only the upper needle was constantly heated. The temperature gradient between the two needles was then recorded. Both needles were installed one above the other at breast height with a vertical distance of 12.5 cm. High xylem sap velocities imply a faster transport of heat and therefore a smaller temperature difference (about 5–15 °C) between the two needles. For each species (*F. sylvatica*, *P. abies*, *A. pseudoplatanus* and *F. excelsior*), we equipped four trees (16 trees in total) with two sap flow sensors, one facing north and the other one facing south. Sap flow sensors were covered with bubble warp aluminum foil to protect them from rain and influences from fluctuations in air temperature. We collected data from April 1, 2012 to December 31, 2013 at 10-min intervals. For each sensor, we calculated sap flow rates after Granier (1985, 1987) and for each tree we averaged the sap flow rates from both sensors to minimize potential thermal effects of sunshine.

For our analyses, we were mainly interested in response patterns of sap flow to changes in soil moisture. Because absolute sap flow rates can vary substantially even within a species as a result of tree height, age, leaf area, stem circumference and other physiological parameters (e.g., wood anatomy and hydraulic conductance) we thus used normalized sap flow rates for our analyses. To normalize the sap flow data, we defined May 15 to September 30 as peak growing season. We defined the highest 2.5% of all sap flow values in peak growing season as maximum values and averaged these values for each individual tree. We then divided the sap flow rates of each individual tree throughout the growing season by its representative averaged maximum values. The values we obtained are referred to as relative sap flow and range from 0 to 1. We performed this normalization procedure separately for the growing seasons 2012 and 2013. Relative sap flow rates of individual trees of a species were finally averaged to calculate species mean relative sap flow rates. We identified midday maximum relative sap flow (10:30–15:30 CET) for each day during the growing season in 2012 and 2013. This procedure allowed us to correlate midday maximum relative sap flow with other variables (i.e., TWD) sorted by the same approach (Figures 3 and 5).

Dendrometer measurements

Throughout the 2012, 2013 and 2014 growing seasons, high-precision point dendrometers (ZN11-T-WP, Natkon.ch, Oetwil am See, Switzerland) recorded stem radius changes at the same trees where sap flow sensors were installed ($n = 16$). Dendrometers were mounted on a carbon fiber frame, which was fixed to the stem into the inactive heartwood by three stainless steel thread rods. A sensing rod was pressed against the bark by the force of a spring. Stem radius changes were measured in 30 s intervals and average values were recorded every 10-min by a data logger (CR1000, Campbell Scientific Inc., Logan, UT, USA). Each tree had one point dendrometer installed at breast height. The temperature sensitivity of the measurement device is <0.3 μm/°C (according to manufacturer) and was not further corrected. The dendrometers measured stem radius changes, which allowed the calculation of TWD and stem increment following the approach by Zweifel et al. (2016). This approach defines radial growth as the difference between the current measured stem radius and the maximum measured stem radius of the past, if the current measured value exceeded the last measured maxima. TWD is defined as the difference between the current measured stem radius and the maximum measured stem radius of the past, when the current measured value is below the last measured maximum. Units of growth and TWD are both in μm. TWD was calculated for 2012 and 2013, whereas we calculated growth for 2012, 2013 and 2014.

As TWD strongly varies with trunk morphology and bark anatomy, absolute values of TWD can be highly variable within individuals of a species and in particular across species. We thus normalized TWD data using the same method that we introduced above for normalizing sap flow rates and calculated averaged normalized values for each species. This was possible in our study as it was the primary objective to define the onset of TWD in a drying forest soil rather than the magnitude of TWD in co-occurring tree species. We refer to normalized TWD values are as relative TWD. We also identified the midday maximum relative TWD value during midday (10:30–15:30 CET) for each day during the growing season 2012 and 2013. To test whether physiological variables behaved differently to midday maximum TWD values or to minimum TWD values during pre-dawn, we selected the minimum relative TWD values during pre-dawn (0:00–7:30 CET) for each day during the growing season periods 2012 and 2013.

Statistical analysis

To test the effect of soil drying on sap flow and TWD, we excluded sap flow and TWD data for rainy and damp days from our analyses because high atmospheric humidity and thus low VPD will lead to low sap flow rates that are not associated with soil drying. Specifically, we only included data into our analyses, from days without precipitation, when daily maximum VPD exceeded 1 kPa and when maximum net radiation exceeded 500 $\mathrm{Wm^{-2}}$. Instead of focusing on individual soil drying events we treated tree physiological (sap flow and TWD) and environmental variables for a growing season as one continuous dataset.

An important task of our work was to identify if the onset of TWD differed among the species (e.g., as a result of the tree's access to different soil water supplies). To identify the thresholds when individual species start to respond in their TWD to decreasing soil moisture, we plotted midday maximum relative TWD against daily mean soil moisture and fitted the following exponential function to the data:

$$\mathrm{TWD} = a e^{\left(\frac{b-\mathrm{SM}}{c}\right)} \qquad (1)$$

Here, TWD is midday maximum relative TWD, SM is daily mean soil moisture (vol%), *a*, *b* and *c* are coefficients (for estimated coefficients see Appendix Table A1). We then derived the first derivate of Eq. (1):

$$\mathrm{TWD}' = -\frac{1}{c} e^{\left(\frac{b-\mathrm{SM}}{c}\right)} \qquad (2)$$

and rearranged Eq. (2) to determine daily mean soil moisture for a given TWD′:

$$\mathrm{SM} = b - c\ \ln(-c\mathrm{TWD}') \qquad (3)$$

With Eq. (3) we were able to determine the soil water values at a given slope of the relationship (TWD′) for each species. Comparing the so-derived SM values for a given slope across the four species allowed us to identify if the onset of TWD differed across species. For our calculations, we selected −0.01, −0.05, −0.1 and −0.18 as values for TWD′. We used a one-way ANOVA to test for statistical differences for SM at a given slope across species assuming equal variances for all species.

We tested if the sum of absolute tree growth differed in the periods of June 11 to September 8 in 2013 when compared with the same periods in 2012 and 2014. Here, we wanted to assess if a period with strong soil drying (2013) compared to periods with little or no soil drying (2012 and 2014, respectively) have an effect on tree growth. To do this we used a one-way ANOVA assuming equal variances for all species.

For all data processing, statistical analysis and graphics we used R 3.1.2 (R Core Team 2014).

Results

Climatic and soil conditions

Annual mean air temperature was slightly warmer in 2012 (9.8 °C) compared with 2013 (9.3 °C) (Figure 1). Annual precipitation sums differed by 156 mm between the two years, with 1243 mm in 2012 and 1087 mm in 2013 (Figure 1). Averaged soil moisture did, however, not differ on average between the two years. We identified one soil drying period in 2012 (July 2–26) and a much longer period in 2013 (June 11 to September 8) (Figure 1). The latter was interrupted by short rain events (average: 5 mm). VPD and temperature increased less pronounced during soil drying in 2012 as compared with 2013. Daily mean soil moisture reached values below 17 vol% in 2013, whereas soil moisture always remained above this value in 2012. When we compared weather data for the two growing seasons (May 15 to September 30) at our sites to the 30-year reference period 1981–2010 we detected that the growing season 2012 was wetter than the long-term mean, with 13% more precipitation, while 2013 was drier with 12% ± 6% less precipitation compared with the long-term mean. The growing season average temperature was slightly warmer for both study years compared to the reference period 1981–2010 (2012: +0.5 °C ± 0.0 °C, 2013: +0.2 °C ± 0.2 °C). VPD also indicated moister conditions in 2012 (+7% ± 3%) and drier conditions in 2013 (−5.5% ± 0.7%) compared with the reference period 1981–2010.

Tree water deficit

All species showed an increase in relative TWD during late summer of both years (Figure 2). In 2013 we detected an overall increase in relative TWD that started in July, and lasted until September 8, when relative TWD exceeded zero most of this time. This pattern was the same for all species and coincided with the decline in soil moisture (Figure 1). Relative TWD was more evenly distributed throughout 2012 then in 2013. When we tested the effects of declining soil moisture on midday maximum relative TWD of the four species for 2012 and 2013, we found that midday maximum relative TWD responded significantly to declining soil moisture in both years (Figure 3). In 2012, this effect was significant only for *P. abies* and *F. excelsior*. However, in 2013 this effect was significant for all four species. Interestingly, the shape of the relationship between soil moisture and midday maximum relative TWD was exponential for all four species, indicating a threshold response of midday maximum relative TWD to declining soil moisture (Figure 3).

To determine if the onset of TWD in response to declining soil moisture differs across species, we identified the soil moisture at pre-defined slopes of the exponential relationship between soil moisture and midday maximum relative TWD and compared the resulting values across the four species (Figures 3 and 4, note the mirrored abscissa). We found no significant differences in the resulting soil moisture values for any of the four species (Figure 4), which indicates that the onset of TWD occurred simultaneously in all four species.

Sap flow

In 2012, tree species showed no obvious decline in sap flow throughout the growing season (Figure 2). Also, when midday maximum relative sap flow rates (i.e., at days with no precipitation, maximum VPD > 1 kPa and maximum net radiation >500 W m^{-2}) were correlated against declining soil moisture or midday maximum relative TWD, we detected no significant relationship for any of the four species in 2012 (Figure 5). In 2013, however, relative sap flow rates decreased in the beginning of July and remained low until the beginning of September, in particular for *P. abies* (Figure 2). When midday maximum relative sap flow rates were tested against declining soil moisture or midday maximum relative TWD, midday maximum relative sap flow of *F. sylvatica*, *P. abies* and *A. pseudoplatanus* decreased significantly with declining soil moisture and midday maximum relative TWD (Figure 5). Interestingly, no response was found for *F. excelsior* (Figure 5). Declining midday maximum relative sap flow in response to declining soil moisture showed a threshold response for all three species in 2013. However, the magnitude of the down-regulation of relative sap flow varied among species (Figure 5): *P. abies* reduced relative sap flow by 92% compared with the growing seasonal maximum, followed by *F. sylvatica* (53%) and *A. pseudoplatanus* (48%). Midday maximum relative sap flow showed a significant negative linear relationship with midday maximum

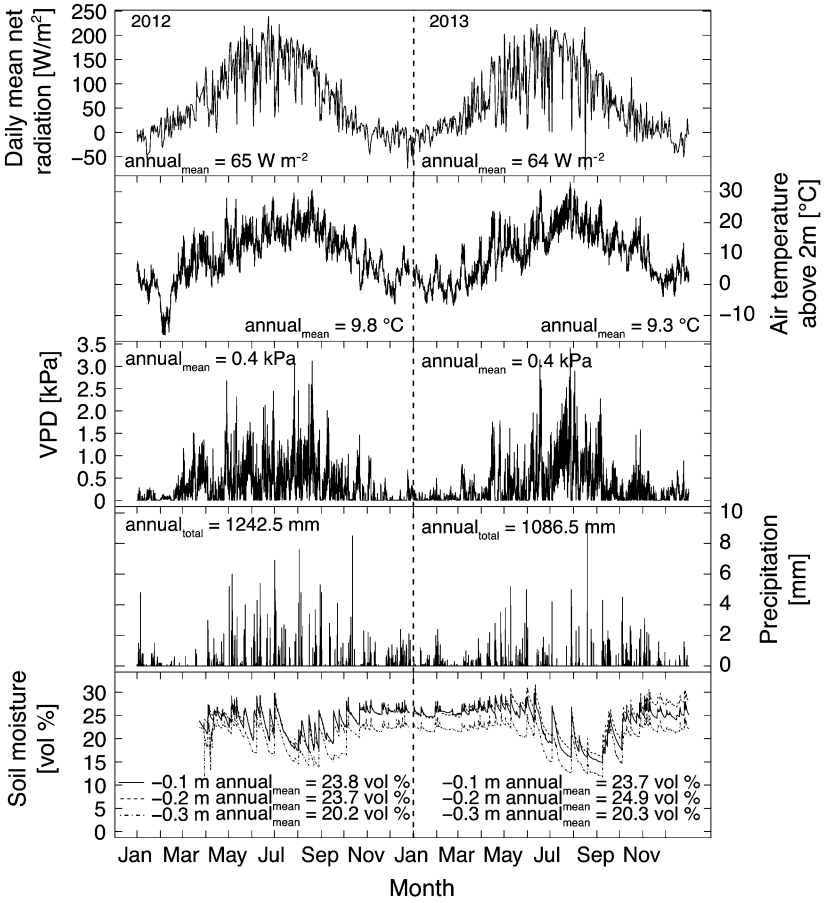

Figure 1. Daily mean net radiation, air temperature measured at 2 m above forest floor, vapor pressure deficit (VPD), precipitation and soil moisture content (at 0.1 m, 0.2 m and 0.3 m soil depth) measured continuously at 30-min resolution during the years 2012 and 2013 at research site Lägeren, Switzerland. Soil moisture content data start in March 2012 due to first sensor installation. All data are presented in 30-min resolution except for net radiation (daily means).

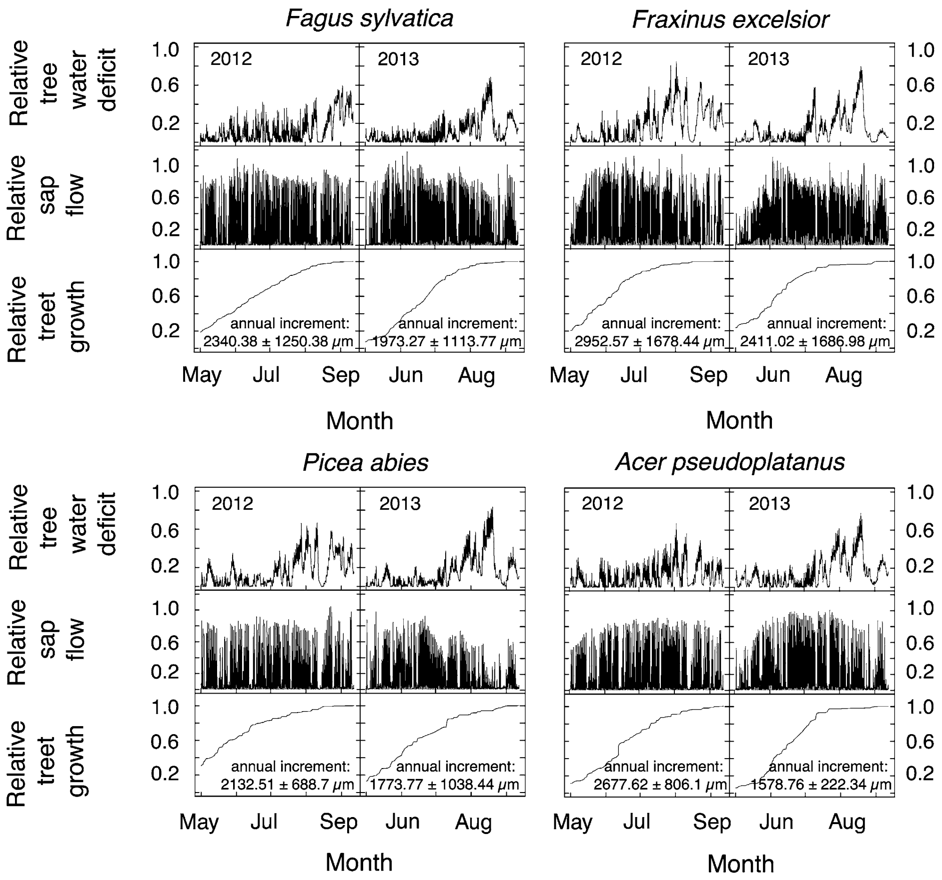

Figure 2. Relative tree water deficit, relative sap flow and relative tree growth during the growing season period (May 15 to September 30) for (a) *P. abies* ($n = 3$ in 2012, $n = 4$ in 2013, $\text{SD}_{\text{rel tree water deficit}} = 0.17$, $\text{SD}_{\text{rel sap flow}} = 0.05$), (b) *F. excelsior* ($n = 4$, $\text{SD}_{\text{rel tree water deficit}} = 0.12$, $\text{SD}_{\text{rel sap flow}} = 0.05$), (c) *F. sylvatica* ($n = 4$, $\text{SD}_{\text{rel tree water deficit}} = 0.25$, $\text{SD}_{\text{rel sap flow}} = 0.04$) and (d) *A. pseudoplatanus* ($n = 4$, $\text{SD}_{\text{rel tree water deficit}} = 0.18$, $\text{SD}_{\text{rel sap flow}} = 0.04$). Tree water deficit, sap flow and tree growth were normalized for both years individually and are presented relative to the 2.5% yearly maximum values (see methods for details).

relative TWD for *F. sylvatica*, *P. abies* and *A. pseudoplatanus* in 2013. Again, *P. abies* showed the strongest reduction in sap flow with increasing TWD, followed by *F. sylvatica* and *A. pseudoplatanus* (Figure 5). In 2012, there was neither a significant correlation between relative sap flow and soil moisture content nor between relative sap flow and TWD for any of the four species.

Tree growth

Relative and absolute radial tree growth showed similar seasonal patterns in 2012, 2013 and 2014. Tree growth commonly accelerated after precipitation events (e.g., after June 29 2013, Figures 2 and 6). We compared the sum of absolute tree growth for the period of June 11 to September 8 in 2013 (i.e., the period of most intensive soil drying) with the corresponding periods in 2012 and 2014 to test if growth differed in corresponding periods either with strong soil drying (2013) and periods with no or little soil drying (2012 and 2014, respectively) (Figure 6). We observed no significant differences in radial tree growth between the three periods in 2012, 2013 and 2014 for either of the species.

Discussion

Summer soil drying triggers a uniform response in TWD in different species

Our data show strong responses of midday maximum relative TWD to declining soil moisture for all four investigated species in 2013 (Figure 3). Interestingly, this response was non-linear, which indicates a threshold response of midday maximum relative TWD to declining soil moisture. Most strikingly, the onset of the midday maximum relative TWD response to declining soil moisture showed no difference across the four investigated species (Figure 3). This became evident, when we compared soil moisture values for given slopes of the relationships between midday maximum relative TWD and soil moisture across the four species (Figures 3 and 4). The observed values were identical across all four species, which indicates that all species were similarly affected in their midday maximum relative TWD by the onset of soil drying. We thus conclude that declining soil moisture in 2013 affected the water supply of all species similarly and that none of the four species was able to fully maintain their water status, e.g., by escaping the declining water availability

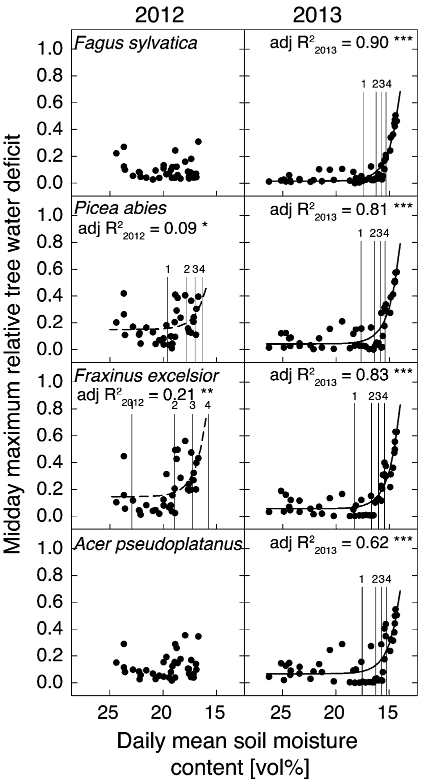

Figure 3. Relationships between midday maximum relative tree water deficit and daily mean soil moisture content (averaged over the top 30 cm soil depth) for the four tree species *F. sylvatica* ($n = 4$), *P. abies* ($n = 3$ in 2012, $n = 4$ in 2013), *F. excelsior* ($n = 4$) and *A. pseudoplatanus* ($n = 4$) in 2012 and 2013. To test the effect of soil drying during the growing season (May 15 to September 30) of the years 2012 and 2013, we only included data into our analysis for days without precipitation, when daily maximum VPD exceeded 1 kPa and daily maximum net radiation exceeded 500 W m^{-2}. The level of significance (***$P < 0.001$, **$P < 0.01$ and *$P < 0.05$) is given for each significant correlation between measurements and exponential fit. Vertical lines numbered with 1, 2, 3 and 4 are the potential soil water content thresholds defined for fixed slopes (1 = –0.01, 2 = –0.05, 3 = –0.1 and 4 = –0.18) of the tangents to the exponential function, which we used to compare species-specific differences in TWD onset in response to soil drying (Figure 4, see methods for details).

through the access of alternative water sources in the soil (for the relationship between soil moisture content and soil water potential see Appendix Figure A1).

The response of midday maximum relative TWD to declining soil moisture differed in 2012 compared to 2013. In 2012, only two species (*P. abies* and *F. excelsior*) showed a significant relationship between soil moisture and midday maximum relative TWD. The explanatory power of these relationships was, however, low. This can be explained by the fact that the 2012 growing season was wetter than the reference period 1981–2010, while the 2013 growing season was drier than the reference period 1981–2010. The patterns we observed in 2012 and 2013 correspond to findings reporting that the relevance of soil water potential and VPD for TWD is changing with increasing levels of dryness, where the impact of soils on TWD increases in growing seasons that are generally dry (Zweifel et al. 2005).

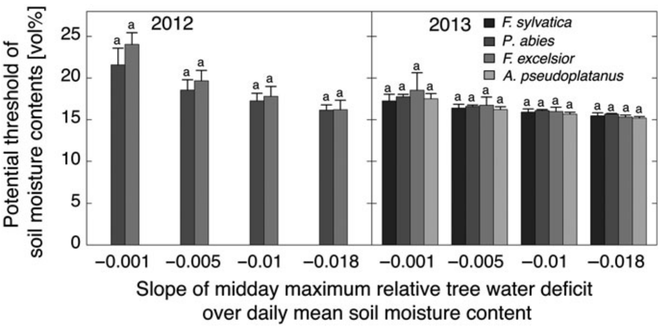

Figure 4. Threshold soil moisture content calculated from the tangents of the exponential fits in Figure 3 for four pre-defined slopes in 2012 and 2013. The four different gray shades indicate the four tree species: *F. sylvatica* ($n = 4$), *P. abies* ($n = 3$ in 2012, $n = 4$ in 2013), *F. excelsior* ($n = 4$) and *A. pseudoplatanus* ($n = 4$). Only cases with a statistically significant fit of the function to the data in Figure 3 were tested. The level of significance (***$P < 0.001$, **$P < 0.01$ and *$P < 0.05$) is given for each significant one-way ANOVA.

Importantly, absolute TWD values can be quite variable within and across species. They are always indicative for the severity of water stress that a tree experiences but they need to be homogenized particularly when comparing different species. In our analysis we used relative TWD values to account for the large within and across species variability and in order to compare TWD patterns across species. We used midday maximum relative TWD values to evaluate when the water status of a tree was affected by declining soil moisture. We were interested in the increased daily water stress a tree experienced during soil drying. We further wanted to relate midday relative TWD to sap flow regulation, which cannot be done with nighttime sap flow values. To test if the use of midday or pre-dawn relative TWD values resulted in different outcomes of our analysis, we yet analysed the relationship between soil moisture and TWD using also values for pre-dawn relative TWD. This analysis revealed no significant difference between midday and pre-dawn values indicating that relative TWD values are a robust proxy for a tree's, water status, independent of diurnal patterns. This observation is in accordance with a study by Drew et al. (2011) who found a strong significant relationship between TWD and leaf water potential using both pre-dawn and midday values.

One minor limitation has to be considered when using TWD to characterize the water status of mature trees. The underlying assumption that no growth occurs during phases of TWD was accounted to cause a bias of 1–5% of the total annual growth (1% in *F. sylvatica*, 5% in *P. abies*) (Zweifel et al. 2016). Despite these uncertainties, the tight relationships between declining soil moisture and midday maximum relative TWD that we observed in 2013 across all species indicate that TWD is indeed a good proxy for estimating the water status of tree. This

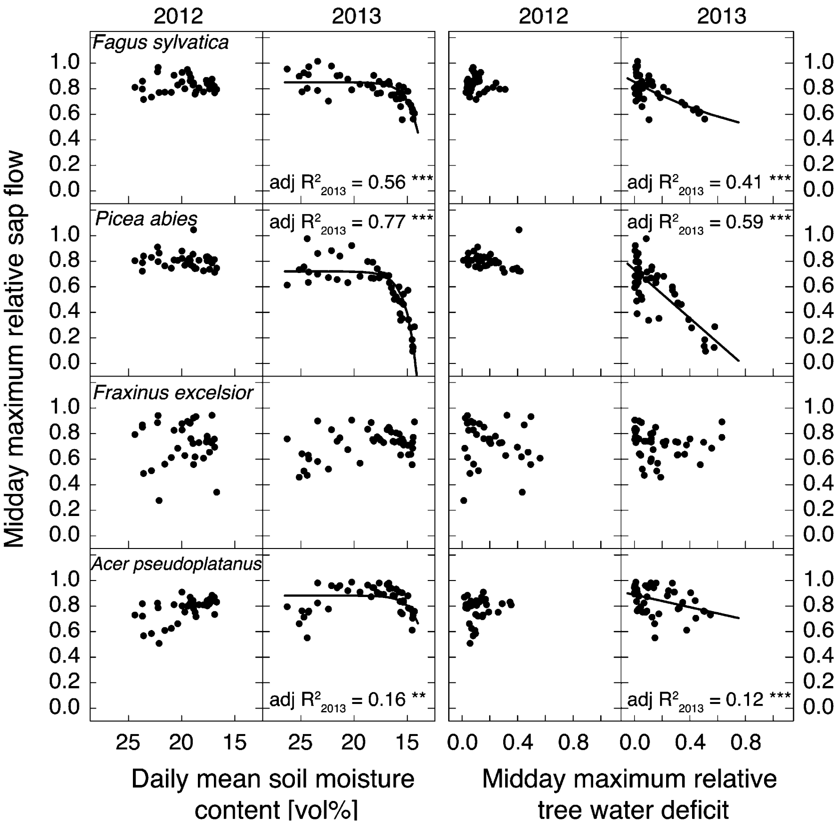

Figure 5. Relationships between midday maximum relative sap flow and daily mean soil moisture content (averaged over the top 30 cm soil depth, $\mathrm{SD}_{\text{daily mean}} = 2.43$ vol%) and midday maximum relative tree water deficit for the four tree species *F. sylvatica* ($n = 4$, $\mathrm{SD}_{\text{midday relative sap flow}} = 0.14$), *P. abies* ($n = 3$ in 2012, $n = 4$ in 2013, $\mathrm{SD}_{\text{midday relative sap flow}} = 0.21$), *F. excelsior* ($n = 4$, $\mathrm{SD}_{\text{midday relative sap flow}} = 0.14$) and *A. pseudoplatanus* ($n = 4$, $\mathrm{SD}_{\text{midday relative sap flow}} = 0.19$) in 2012 and 2013. To test the effect of soil drying during the period from May 15 to September 30 of the years 2012 and 2013, we only included data from days without precipitation when daily maximum VPD exceeded 1 kPa and daily maximum net radiation exceeded 500 W m^{-2}. No best-fit curve is shown for insignificant model fits. The level of significance (***$P < 0.001$, **$P < 0.01$ and *$P < 0.05$) is given for each significant model fit.

is in particular true when not relying on absolute values of TWD but rather on the normalized TWD courses or the onset of relative TWD values in response to changes in an environmental driver such as soil moisture as shown here (Figure 3).

Species differ in their sap flow response to soil drying

Midday maximum relative sap flow rates showed no trend when related to soil moisture or midday maximum relative TWD in 2012 (Figure 5). In contrast, decreasing soil moisture and increasing midday maximum relative TWD both led to a reduction in midday maximum relative sap flow in three out of four species in 2013. We interpret declining sap flow rates as a reduction of the tree's stomatal conductance with the purpose to conserve water and to avoid critically low water potentials that would put a tree at risk of hydraulic failure (Schulze and Hall 1982, Choat et al. 2012). We found marked differences in the response of midday maximum relative sap flow rates to declining soil moisture and to increasing midday maximum relative TWD among the four investigated species. *P. abies* reduced its midday maximum relative sap flow by 92% compared to 53% in *F. sylvatica* and 48% in *A. pseudoplatanus*. *P. abies* responded therefore most sensitively to decreasing soil moisture or increasing midday maximum relative TWD, followed by *F. sylvatica* and *A. pseudoplatanus*. *F. excelsior* showed no response. This sensitive behavior of *P. abies* to declining soil moisture is in accordance with findings from other studies where in particular *P. abies*, but also *F. sylvatica* and *A. pseudoplatanus* were identified as drought sensitive or water demanding species (Lemoine et al. 2001, Leuzinger et al. 2005, Gessler et al. 2007, Koecher et al. 2009, Levesque et al. 2013, Pretzsch et al. 2013). On the contrary, *F. excelsior* was found to show a low drought sensitivity also in previous studies (Scherrer et al. 2011).

The strong influence of declining soil moisture on midday maximum relative TWD and sap flow is interesting also in the context of the increasing number of studies, where drought events in forests are experimentally simulated. As atmospheric vapor cannot be controlled in such studies (Belien et al. 2014), it has been argued that eliminating precipitation would not be sufficient to induce drought stress in mature trees. Our data show clearly that declining soil moisture alone is sufficient to trigger strong physiological responses in trees, e.g., by down regulating their sap flow.

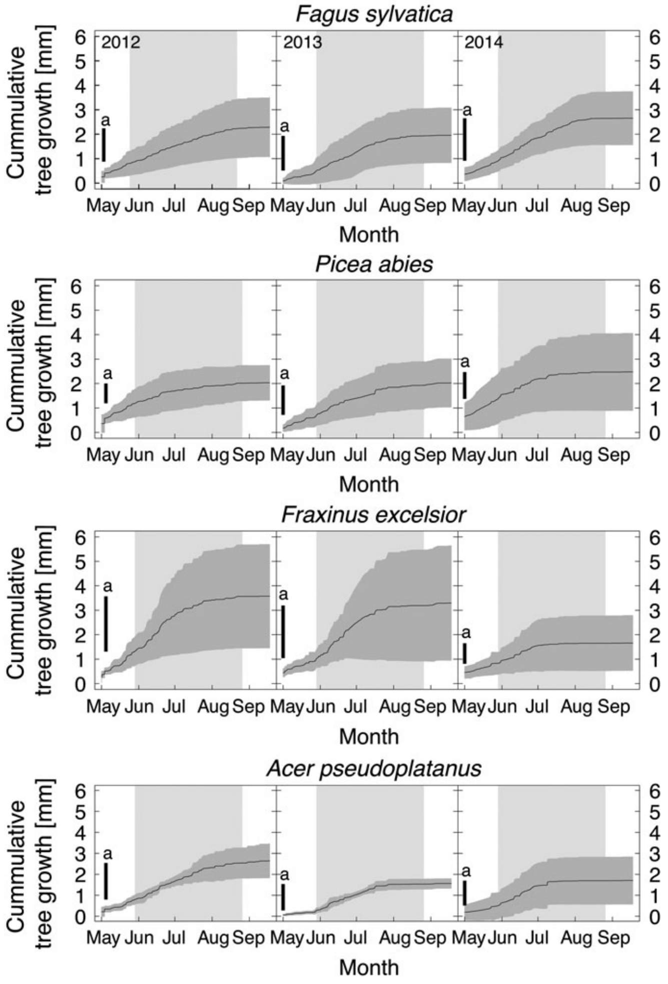

Figure 6. Cumulative tree growth [mm] for *F. sylvatica* ($n = 4$), *P. abies* ($n = 3$ in 2012, $n = 4$ in 2013, $n = 3$ in 2014), *F. excelsior* ($n = 4$) and *A. pseudoplatanus* ($n = 4$) during the 2012, 2013 and 2014 growing season (May 15 to September 30). The dark gray color indicates the standard deviation of the mean (black line) and the black vertical bar indicates the absolute tree growth for the period from June 11 to September 8 in 2012, 2013 and 2014, which we detected as the driest period in 2013. The level of significant differences in absolute tree growth between the three years (***$P < 0.001$, **$P < 0.01$ and *$P < 0.05$) is given for each significant one-way ANOVA.

Species show different strategies to cope with declining soil moisture

Our study corroborates previous findings with respect to the species-specific sensitivity of sap-flow in temperate tree species in response to declining soil moisture or drought (Pataki et al. 2000, Holscher et al. 2005, Koecher et al. 2009). The most severe impact of declining soil moisture on the functioning of a tree is the vulnerability of its xylem to cavitation. The vulnerability of a species to cavitation is typically described as the water potential where a tree loses 50% of its conductivity, the so-called P50 values. P50 values and thus xylem vulnerability to cavitation can be very different for different tree species (Klein 2014). For the species we investigated in the context of our study, Klein (2014) suggests P50 values for *P. abies* abies to be −4.0 MPa, −1.6 MPa for *A. pseudoplatanus* and *F. excelsior* and *F. sylvatica* slightly less sensitive (−2.8 and −3.2 MPa, respectively). Based on these values one could expect reductions in sap flow in *A. pseudoplatanus* before reductions in *F. excelsior* and *F. sylvatica*, with *P. abies* being the last to respond. Evidently this is not the case in our study. It is, however, important to note, that our study does not allow any conclusions about the severity of water stress that the different species have experienced and thus if their foliar water potentials approached the species-specific P50 values. In fact, midday leaf water potentials can be quite different across species that experience the same soil moisture because the hydraulic conductivity of the tree is also a major driver of foliar water potentials. It is therefore possible, that *P. abies* experienced the most negative foliar water potentials in our study and thus responded most sensitively to declining soil moisture. Although we have not determined foliar water potential in our study, the sap-flow responses to declining soil moisture that we show here in combination with the data provided by Klein (2014) suggest that *P. abies* approaches critical levels of its water status earlier than *A. pseudoplatanus*, *F. sylvatica* and in particularly *F. excelsior* and is thus the first to adjust its sap flow rates.

A common explanation in the literature why temperate tree species differ in their drought sensitivity has been that trees differ in their rooting depth and are thus differently affected by declining soil moisture. In particular it has been suggested that *Q. petraea* and *F. excelsior* have access to deeper and more persistent water sources in the soil (Koestler et al. 1968, Leuzinger et al. 2005, Koecher et al. 2012) and are thus not as strongly affected by dry spells than shallow rooted *P. abies* trees (Ellsworth and Sternberg 2015). Based on this explanation, we expected to find a delayed onset of TWD in those species that also showed a low sensitivity of sap flow to declining soil moisture, i.e., *F. excelsior* (Cuevas et al. 2010). However, we did not detect such delayed onset of midday maximum relative TWD for any of our four species (Figures 3 and 4). In contrast, our analyses showed that declining soil moisture affected the water status of all species at the same time (Figure 4). It seems therefore unlikely that species with a presumably deep rooting system such as *F. excelsior* can fully escape or avoid the impact of soil drying on their water relations but that these species are also affected in their water relations by drying soils. It is, however, possible that species with a presumably deep rooting system can yet sustain their water status during extended dry periods well above critical limits (i.e., above their P50 values) and are thus less conservative in regulating their water relations.

In addition, differences in the species' hydraulic properties can also contribute to the sensitivity of a species to declining soil moisture. Hydraulic properties are governed, among others, by their different wood anatomies (ring-porous: *F. excelsior*; diffuse-porous: *A. pseudoplatanus*, *F. sylvatica*; coniferous: *P. abies* (Fritts 1976)) and therefore different patterns of conduit distribution and complexity of cell types (McCulloh et al. 2010). These differences in wood structure and the consequential differences in the risk of hydraulic failure at a given water supply in the soil could be a reason why these four temperature tree species differ in their stomatal control as soil moisture declines (Choat et al. 2012).

We observed that *F. excelsior* did not respond in its midday maximum relative sap flow to declining soil moisture in 2013. Similar observations have been made for other ring-porous species, in particular for deciduous oak species in European and North American forests (Leuzinger et al. 2005, Zweifel et al. 2007, Koecher et al. 2009, McCulloh et al. 2010, Meinzer et al. 2013, Klein 2014). Low drought sensitivity of ring-porous species has been observed despite their large vessel diameters, which would suggest a high vulnerability to cavitation. A generally accepted explanation why ring-porous species seem to be less responsive to declining soil moisture and are thus considered more drought tolerant than diffuse-porous species does not currently exist in the literature. Koecher et al. (2012) showed that root and stem xylem anatomy do not necessarily have to resemble. They found *F. excelsior* xylem to be ring-porous while its roots were not and that the smaller root vessels suggest a high hydraulic resistance in the hydraulic system of *F. excelsior*. The authors suggest that *F. excelsior* compensates the low conductivity in individual roots with a large fine root biomass (Koecher et al. 2012). The extensive root system of *F. excelsior*, and the resulting access to a larger soil water pool, might help explaining why sap flow rates in *F. excelsior* remained constant despite declining soil moisture.

In this context it is also important to note that sap flow rates, and in particular the midday maximum relative sap flow rates that we show here, give no indication on the absolute water consumption of a tree. When absolute rates of water flow (i.e., sap flow density unit) were compared among deciduous European tree species, it was shown that *F. excelsior* had lower rates compared to *F. sylvatica* and *A. pseudoplatanus* (Lemoine et al. 2001, Holscher et al. 2005, Gebauer et al. 2012). In accordance, *F. sylvatica* and A. *pseudoplatanus* also have larger leaf areas than typically found in *F. excelsior* (Koecher et al. 2012). It seems that *F. excelsior* has therefore a more conservative whole-tree water consumption than other co-occurring species and consequently needs less down-regulation in times of declining water supplies.

Growth patterns during summer soil dryings in 2012, 2013 and 2014

Despite substantial differences among temperate species in their sap flow responses to declining soil moisture, we could not find any significant difference in tree growth (deduced from absolute stem radius increments over a year) when comparing the soil drying in 2013 to the same period in 2012 and 2014 for any of the four species (Figure 6). Interestingly, Leuzinger et al. (2005) found reduced basal stem area in all investigated species (*F. sylvatica*, *Q. petraea*, *C. betulus*, *Tilia playtyphyllos* and *Acer campestre*) in the extreme summer drought in 2003. Also, Zielis et al. (2014) demonstrated that the previous year's climatic conditions in spring have a significant impact on growth in the current year. Our study does not show such lag effects. We speculate that the impact of soil drying in 2013, which occurred at the end of the growing season, may not have been strong enough to leave a signal in the annual growth response. Also, soil drying in 2013 occurred when the majority of annual increment in tree growth was already completed (Figure 6). The intensity, duration and the timing of the soil drying could explain why no significant growth reduction basal area increment in any of the four species was observed in the relatively dry year 2013 and neither in the subsequent year (2014).

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Conflict of interest

There is no conflict of interest.

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Appendix

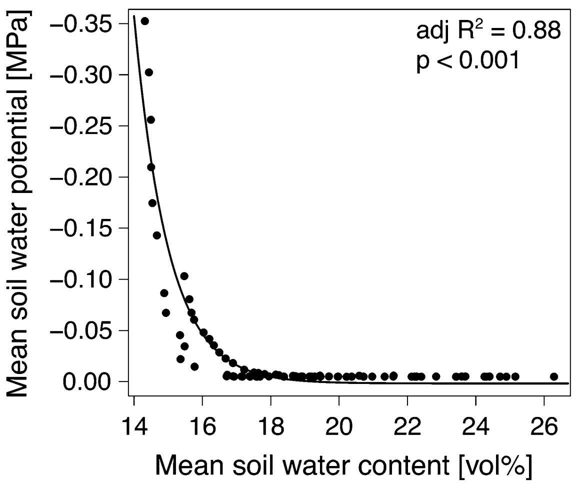

Figure A1. Relationship of mean soil water content (averaged over 0.1, 0.2 and 0.3 m soil depth) and mean soil water potential (averaged over 0.05, 0.1, 0.15, 0.2 and 0.3 m soil depth) at Lägeren research site during the growing season period from May 15 to September 30 in 2012 and 2013 when we excluded rainy and damp days, i.e., we only included data from days without precipitation when daily maximum VPD exceeded 1 kPa and daily maximum net radiation exceeded 500 W m^{-2}.

Table A1. Estimates with standard error for the coefficients *a*, *b* and *c* of the exponential function describing the relationship between TWD and soil moisture content: TWD $= ae^{(\frac{b-\mathrm{SMC}}{c})}$. To estimate the coefficients, we defined a model with parameters varying in a natural range, with lower bounds set to $a = 0.01$, $b = 10$ and $c = 0.1$.

Individuals	Coefficient *a*	Coefficient *b*	Coefficient *c*
P. abies	2012		
8001	0.030 ± 0.124	14.567 ± 2.073	2.212 ± 2.182
8005	NA	NA	NA
8006	0.154 ± 0.019	16.525 ± 0.356	0.100 ± 1.847
J	0.166 ± 0.056	13.730 ± 4.600	1.539 ± 2.182
F. excelsior	2012		
2586	0.125 ± 0.179	14.664 ± 1.859	2.674 ± 2.751
2591	0.010 ± 0.146	15.220 ± 0.967	2.591 ± 1.828
8010	0.078 ± 0.018	16.577 ± 0.147	0.100 ± 0.103
8015	0.060 ± 0.059	12.963 ± 2.297	2.617 ± 1.754
F. sylvatica	2013		
2632	0.035 ± 0.025	14.100 ± 0.100	0.866 ± 0.158
2577	0.033 ± 0.017	14.242 ± 0.046	0.645 ± 0.084
8003	0.010 ± 0.006	13.678 ± 0.081	0.642 ± 0.063
8007	0.040 ± 0.004	10.000 ± 1.463	1.498 ± 0.478
P. abies	2013		
8001	0.010 ± 0.011	14.200 ± 0.035	0.634 ± 0.060
8005	0.026 ± 0.014	14.200 ± 0.037	0.715 ± 0.066
8006	0.090 ± 0.018	10.000 ± 13.641	1.212 ± 3.629
J	0.104 ± 0.032	14.200 ± 0.098	0.772 ± 0.174
F. excelsior	2013		
2586	0.300 ± 0.010	13.752 ± 0.117	0.704 ± 0.105
2591	0.031 ± 0.014	14.057 ± 0.064	0.815 ± 0.094
8010	0.166 ± 0.034	13.585 ± 0.462	0.750 ± 0.368
8015	0.043 ± 0.027	13.343 ± 0.242	2.166 ± 0.375
A. pseudoplatanus	2013		
2585	0.054 ± 0.027	13.731 ± 0.232	0.977 ± 0.257
2587	0.117 ± 0.028	13.518 ± 0.612	0.758 ± 0.406
8011	0.138 ± 0.032	13.402 ± 0.502	0.929 ± 0.400
8012	0.037 ± 0.013	13.957 ± 0.090	0.548 ± 0.092