

# Drought-sensitivity ranking of deciduous tree species based on thermal imaging of forest canopies

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## ABSTRACT

Most climate change projections for Central Europe predict higher mean summer temperatures and prolonged summer drought periods. However, in diverse mixed forest stands we expect tree species specific responses to water shortage, as tree species are highly variable in rooting depth and physiological traits related to the water balance. Here, we assessed the drought sensitivity of the water relations of six deciduous forest tree species at four sites with contrasting water availability by airborne thermal imagery of canopy foliage temperature, sap flow and soil water potential. Canopy architecture had a consistent influence on canopy foliage temperature with 'dense canopy' species (*Acer pseudoplatanus*, *Fagus sylvatica* and *Tilia platyphyllos*) being warmer (0.5–1.5 K) than 'open canopy' species (*Fraxinus excelsior*, *Prunus avium* and *Quercus petraea*). While the canopy foliage was close to air temperature at the beginning of the drought period ( $\Delta T_{C-A} = -0.1$  to 0.7 K) it strongly warmed up with ongoing drought, especially at the two 'dry' sites with a  $\Delta T_{C-A}$  of 3.5–5 K. The pronounced canopy foliage warming at the 'dry' sites after 22 days of drought was associated with reduced transpiration rates as sap flow was curtailed by 20–35% in all species except *F. excelsior* and *Q. petraea*. Based on canopy foliage temperature and sap flow data, we considered *A. pseudoplatanus* the most drought sensitive species followed by *F. sylvatica*, *T. platyphyllos* and *P. avium* and the two ring-porous species *F. excelsior* and *Q. petraea* being clearly the least sensitive ones. At drier sites, increasing summer temperatures and drought might change the competitive abilities of tree species in favour of those that are able to maintain transpirational fluxes and cooler canopies such as *F. excelsior* and *Q. petraea*.

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## 1. Introduction

Plant species composition of communities and productivity strongly depend on water availability anywhere on the globe (Schulze et al., 1996; Kreft and Jetz, 2007). European temperate forests are composed of species that differ in their moisture requirements (Ellenberg, 1974). As most climate change projections for Central Europe predict lower summer precipitation with prolonged drought periods (Christensen et al., 2007) water availability will become critical for some taxa. Regional projections for Switzerland indicate a 20% decrease in summer precipitation and 4 K higher mean summer temperatures in 2070 (Frei et al., 2006; Meehl et al., 2007). The higher summer temperatures in combination with high atmospheric vapour pressure deficits (vpd) will

lead to higher evaporative demand and therefore will exert higher water demand and, thus, a greater likelihood of water shortage. Forest tree species are highly variable in rooting depth, canopy architecture and physiological traits related to the water balance (Canadell et al., 1996; Dawson, 1996; Jackson et al., 1996; Schulze et al., 1996; Schenk and Jackson, 2002; Körner, 2005). The species specific responses to the expected climate change might therefore alter the competition among species (Leuzinger et al., 2005; Zweifel et al., 2009) and lead to new community compositions (Gessler et al., 2007; van Mantgem and Stephenson, 2007). As most forests in Central Europe are actively managed (timber production) these changes are not only biologically important (Adams et al., 2009; Allen et al., 2010) but will also have socio-economic consequences (Millennium Ecosystem Assessment, 2005). Even if the species composition might stay the same, species specific changes in fitness directly influence the timber harvest. As the seedlings of today will be the forest of 2100, information about tree responses to climate change are essential for both biological and economic (forestry) planning.

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Most studies dealing with drought effects on plant species communities either work with single extreme events such as for example the hot and dry summer 2003 (e.g., Weaver et al., 1935; Bollinger et al., 1991; Stämpfli and Zeiter, 2004; Czajkowski et al., 2005; Leuzinger et al., 2005; Archaux and Wolters, 2006; Low et al., 2006; Reichstein et al., 2007), experimentally with rainout shelters (e.g., Sternberg et al., 1999; Grime et al., 2000; Köchy and Wilson, 2004; Morecroft et al., 2004; Gilgen and Buchmann, 2009) or throughfall exclusion experiments (e.g., da Costa et al., 2010; Markewitz et al., 2010). While rainout shelters allow exerting different controlled conditions over several years they are only practicable for low stature vegetation such as grasslands, dwarf shrubs and small areas. Studies working on mature forest stands with 50–100 year old trees and 30 m canopy height, as the one presented here, are mostly limited to observations during drought periods or confined to relatively small areas (given the ca. 100 m<sup>2</sup> of a single tree crown). Broad airborne screening offers the replication and spatial coverage needed to allow conclusion on an ecosystem level.

A non invasive method to gain information about the water status of a plant is thermal imaging of leaves or canopy foliage as a proxy for the energy balance and, thus, for concurrent transpiration (Fuchs, 1990; Jones, 1999a; Jones and Leinonen, 2003; Leinonen et al., 2006). Canopy foliage temperature is a resultant of the energy balance (net radiation – latent heat flux – sensible heat flux) at leaf level and is dominated by plant architecture (canopy shape, canopy density, leaf size, boundary layer resistance, etc.), environmental conditions (incoming radiative energy, air temperature, wind) and plant-controlled transpiration (Monteith and Unsworth, 1990). Adequate information on these essential parameters is imperative to evaluate the actual water status of a tree, especially when ‘dry’ and ‘wet’ reference surfaces are missing (Jones et al., 2002). However, as the architecture of an individual tree only changes marginally during a few weeks of drought in mid-summer, relative comparisons (in time) are possible. On bright, warm days the canopy foliage temperature to air temperature difference ( $\Delta T_{C-A}$ ) is mainly the result of transpiration (Fuchs, 1990; Jones, 1999b). By revisiting selected trees or forest sites under similar weather conditions (incoming radiative energy, wind) the  $\Delta T_{C-A}$  yields direct estimates of the relative changes in transpiration. To ensure that the changes in  $\Delta T_{C-A}$  are connected to changes in transpiration, and therefore water status, direct measurements such as stomatal conductance or sap flow are essential (Jones and Leinonen, 2003; Leuzinger et al., 2005; Leuzinger and Körner, 2007b). Unfortunately, these direct methods are expensive or too time consuming to cover many trees, whereas thermal imagery allows to collect huge amounts of data in a short time over very large areas. There remains an elusive problem: trees that are highly sensitive to vpd reduce their transpiration by diminishing stomatal conductance even under favourable soil water conditions. Hence, neither flux nor canopy temperature can reveal with certainty whether a tree suffers from water shortage (Körner, 1985). In the current study, we can identify such responses during the earliest part of the hot summer period when soils were still wet, but vpd quite high. A species performing such pronounced vpd response should show a flux reduction and canopy warming relative to others at this early stage.

In this study we combined airborne thermal imagery of canopy foliage temperature with ground based measurements of sap flow and soil water potential in diverse mixed forest patches with contrasting water availability, (1) to analyse species specific differences in canopy foliage temperature due to leaf and canopy architecture, (2) to establish and compare a ‘ranking’ of tree species according to their canopy foliage temperature at sites and periods with contrasting water availability, and (3) to explore the relevance of thermal image data with regards to tree-specific actual sap flow and soil moisture.

## 2. Materials and methods

### 2.1. Study sites and species

In total, we had two different temperate-lowland test regions, namely: Hofstetten-Flüh (47°28′N, 7°30′E; elevation 550 m a.s.l.) and Münchenstein (47°30′N, 7°37′E; elevation 350 m a.s.l.) both in the NW part of Switzerland. Within each test region we searched for diverse mixed forest stands on flat terrain (no exposition) that were at least 50 years old and had a closed canopy. Out of these potential study sites we then chose for each test region one site we expected to dry out fast during a drought period (in the following called ‘dry’ site) and one site we expected to stay rather moist also during prolonged drought (in the following called ‘moist’ site). The selection of the two ‘dry’ and ‘moist’ sites was based on long term expert knowledge of local foresters and indicator species present in the understorey (Landolt, 1977).

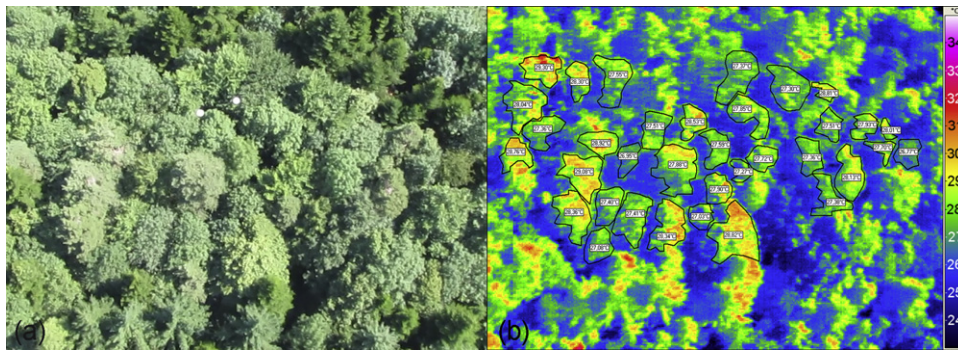
The forest stands at all four study sites are dominated by *Fagus sylvatica* L. (European beech) and *Quercus petraea* (Matt.) Liebl. (sessile oak), with *Acer campestre* L. (field maple), *Acer pseudoplatanus* L. (sycamore), *Carpinus betulus* L. (European hornbeam), *Fraxinus excelsior* L. (European ash), *Prunus avium* L. (wild cherry) and *Tilia platyphyllos* Scop. (large-leaved lime) present as companion species. In addition, at all sites we found several conifer species (*Abies alba* Mill. (European silver fir), *Larix decidua* Mill. (European larch), *Picea abies* L. (Norway spruce), *Pinus sylvestris* L. (Scots pine)). In the study presented here, we selected *A. pseudoplatanus*, *F. sylvatica*, *F. excelsior*, *P. avium*, *Q. petraea* and *T. platyphyllos* as these species were present at all sites with at least three large canopy forming individuals and represent important elements of the temperate mixed forests found in Central Europe.

As all study sites are within 15 km they share the same temperate zone climate, characterized by mild winters and moderately warm summers. The growing season usually lasts from end of April to the end of October (ca. 180 days, Asshoff et al., 2006). The long-term annual precipitation at the study sites is 990 mm and the mean January and July temperatures are 2.1 and 19.1 °C. In the study year 2010 the precipitation during the growing season (May–October) was 512 mm and therefore about 15% less than the long term average of 600 mm.

### 2.2. Climatic data and soil water potential

Air temperature, relative humidity, rainfall, solar radiation and wind speed were measured by an official weather station (MeteoSwiss, Binningen weather station, 316 m a.s.l.) in close distance to our study sites at Münchenstein (<4 km). A second weather station was located at Hofstetten-Flüh above the tree canopy at the top of a construction crane (Vantage Pro2 Plus with a solar radiation sensor; Davis Instruments, Hayward, CA, USA). Climate data was recorded continuously at a 10-min resolution from June to mid August. Air temperatures for all study sites were calculated from the weather station data by a simple correction for differences in elevation (0.6 K per 100 m of elevation). In addition, during the thermal imaging campaigns the air temperature and relative humidity at all sites was measured within the canopy by small data loggers (Hobo U08, Onset computer corporation, Bourne, MA, USA) attached to a helium balloon. The site specific vapour pressure deficit (vpd) during the thermal imaging campaigns was calculated based on the relative humidity and air temperature recorded within the canopy.

Soil water potential, at 10 cm soil depth, was recorded by three sensors (MPS-1, Decagon Devices Inc., Pullman, WA, USA) per site (12 sensors in total) and logged at a 5-min temporal resolution using a wireless multichannel data logging system (DecentNet, Decentlab, Dübendorf, Switzerland).



**Fig. 1.** (a) An example of a visual light image of a diverse mixed forest patch ('moist' site, Hofstetten-Flüh) and (b) the same image section as a thermal image. The polygons mark individual tree canopies and the numbers indicate the mean canopy foliage temperature. Both images were recorded on 17 July 2010 14:30 at an air temperature of 31 °C. Note the two helium balloons in the canopy which carry temperature and humidity sensors and at the same time mark the location where ground data are collected.

### 2.3. Sap flow measurements

Sap flow measurements were conducted on two individual trees per species and site ( $2 \times 6 \times 4 = 48$  trees in total). We used 'Granier-type' sap flow sensors (Granier, 1985), that consisted of two 20 mm long and 2 mm diameter probes (coated with heating wire) inserted into the sapwood (after removal of the bark) at breast height with a vertical spacing of 15 cm (UP, Kolkowitz, Germany). Sensors were protected against water and strong thermal fluctuations using Styrofoam pads and silver foil bubble wrap insulation. Readings were taken at 10 s intervals and aggregated as 5 min means, using a wireless multichannel data logging system (DecentNet, Decentlab, Dübendorf, Switzerland). The sap flow raw data in millivolt signals were first standardized according to Granier's empirical formula (Granier, 1985; Steppe et al., 2010) and converted into tree specific 'relative' sap flow (values between 0 and 1), with 1 being the tree specific maximal sap flow observed during the measurement period (June to mid August) and 0 representing minimum or no sap flow (mostly during late night, early morning). The sap flow measurements were continuous from June to mid August but in this study we only discuss the fraction of sap flow data recorded during to the thermal imaging campaigns.

### 2.4. Thermal imaging campaigns

During a four week drought period (24 June to 22 July) we conducted three thermal imaging campaigns on bright weather during noon. Canopy foliage temperatures were recorded using a thermal camera (VarioCam, Infratec, Dresden, Germany) with a resolution of  $240 \times 320$  pixels, providing 76,800 temperature readings at a 0.1 K resolution. The measurements were taken from a helicopter flying ca. 100 m above the canopy, with a spatial resolution of ca.  $350 \text{ cm}^2/\text{pixel}$ . All three thermal imaging campaigns took place between 13:00 and 14:30 h (true local time, highest insolation) and covered all four study sites (flight time ca. 45 min). To assure similar weather conditions (particularly solar radiation and wind) for all sites we only flew on cloud-free days with very little wind. The first thermal imaging campaign was conducted one week after the last rain fall on 02 July followed by approximately one flight per week depending on optimal weather conditions (07 July, 17 July).

To ensure the identification of individual trees within the thermal images we attached a high definition video camera to the thermal camera. We recorded thermal images at a frequency of 5 Hz and at the same time visual light images at 30 Hz. By aligning the two series of images (by time stamp) we were able to identify the individual trees in the high resolution visual light images and apply this information to the corresponding thermal images (sample image Fig. 1). The white helium balloons in the canopy assisted in geo-referencing tree crowns at the experimental sites.

### 2.5. Data processing and statistical analysis

For all flights and study sites we extracted as many canopy foliage temperatures of individual trees as possible from the thermal images. We selected sun exposed canopy fractions and disregarded clearly shaded parts. As the quantitative species composition of the study sites as well as the flight path of the helicopter slightly differed, the number of individual trees per species/site varied. This resulted in 3–10 individual trees per species and site for the statistical analysis (184 trees in total). The relative canopy foliage temperature ( $\Delta T_{C-A}$ ) was calculated as the difference between canopy and air temperature at the site. The standardization by current air temperature allowed us to compare different sites and imaging campaigns even if there was a difference in absolute air temperature, given that the deviation of leaf temperature from air temperature is mostly driven by tree architecture and transpiration under cloud and wind free conditions. In addition to the mean canopy foliage temperature of each individual tree we also measured the maximum and minimum value within the selected polygons (tree crowns). For all the analysis of thermal images, Irbis professional (Infratec, Dresden, Germany) was used.

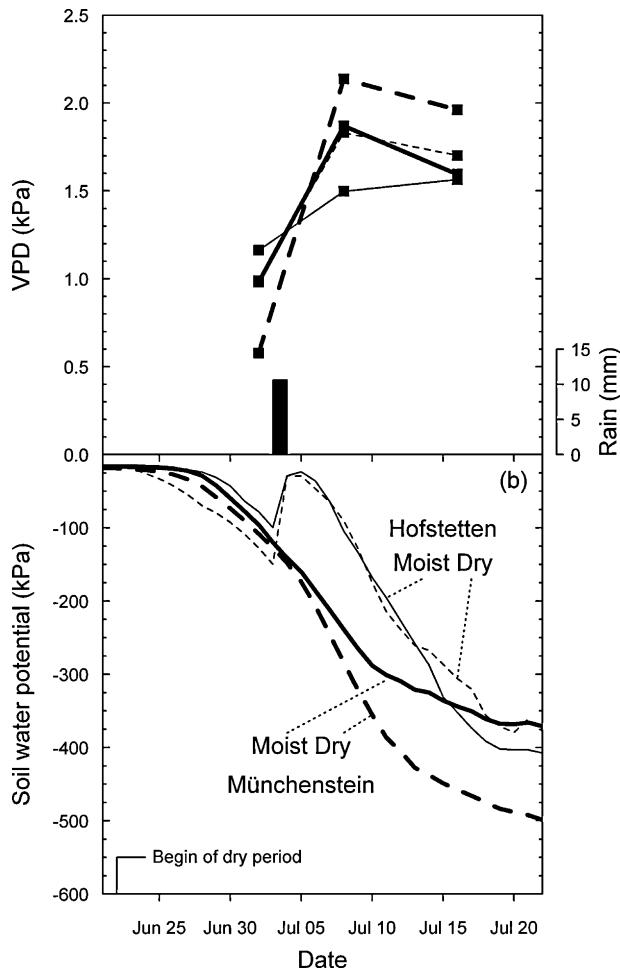
In a first step we used linear mixed-effects models to test the impact of 'duration of dry period' and 'study site' on ' $\Delta T_{C-A}$ '. In a second step we used a linear mixed-effects model to assess the species specific differences in canopy foliage temperatures. As we assumed these species specific differences to be mostly dependent on leaf and canopy architecture, 'study site' as well as 'duration of dry period' should be of minor importance and were therefore treated as random factors. Based on the output of this model we then grouped the tree species according to their 'canopy architecture' (based on significant differences) into two groups: 'dense canopy' (*A. pseudoplatanus*, *F. sylvatica*, *T. platyphyllos*) and 'open canopy' (*F. excelsior*, *P. avium*, *Q. petraea*). As a last step, we used a linear mixed-effects model with restricted maximum likelihood to check if different 'plant species' reacted similar to the drought period. To do so we used 'duration of drought period', 'water availability' ('moist', 'dry' site) and 'plant species' as fixed factors including all possible interactions.

For all data processing, statistical analyses and graphics, R 2.12.1 (R Development Core Team, 2010) was used.

## 3. Results

### 3.1. Weather conditions and soil water potential

In 2010, the average air temperature in July was 20.9 °C, which is 1.8 K higher than the long term average, indicating a warm and dry July with no rain fall from 24 June to 22 July at the study sites in Münchenstein and only a small rain event (10.6 mm on 4 July) at



**Fig. 2.** (a) Mean vapour pressure deficit (vpd) during the three thermal imaging campaigns (02 July, 07 July and 17 July) for all four study sites. The black bar indicates the small rain event at the sites in Hofstetten-Flüh. (b) The course of soil water potential late during the drought period (21 June to 22 July) at all four study sites (means of three sensors per site). Solid lines are 'moist', dashed lines are 'dry' sites, bold lines are for the moist/dry pair in Münchenstein and fine lines are for the moist/dry pair in Hofstetten-Flüh.

the study sites in Hofstetten-Flüh (Fig. 2). During our three thermal imaging campaigns the concurrent air temperatures were ca. 30.5, 31 and 31 °C. The combination of high air temperatures and dry weather conditions led to high vpd with up to 2.2 kPa towards the end of the drought period (Fig. 2). The soil water potential at the study sites in Münchenstein decreased continuously from 24 June to 22 July while at the Hofstetten-Flüh study sites there was a brief reset of the soil water potential on 4 July (Fig. 2). At all study sites the soil water potential in 10 cm soil depth was very low towards the end of the drought period ranging from –380 to –500 kPa (the detection limit of the sensor).

### 3.2. Canopy foliage temperatures

The relative canopy foliage temperatures showed significant differences among 'study sites' and 'duration of the drought period' (thermal imaging campaigns) including a significant interaction (Table 1). There was no difference among the sites at the beginning of the drought ( $P=0.69$ , data of 7 July) with mean canopy foliage temperatures close to air temperature at all sites ( $\Delta T_{C-A} = -0.1$  to 0.7 K, Table 2). After 13 and 22 days of drought the canopy foliage temperature of the two 'dry' sites were significantly higher than the two 'moist' sites ( $P<0.001$ ) and considerably higher than air temperature ( $\Delta T_{C-A} = 3.5$ –5.0 K, Table 2).

**Table 1**

Results of a two-way ANOVA on the effects of study site and duration of the drought period on the relative canopy foliage temperature ( $\Delta T_{C-A}$ ).

Factor	Df	F	P
Site	3, 180	112.4	<0.001
Drought	2, 236	330.7	<0.001
Site $\times$ drought	6, 236	71.5	<0.001

Df, degrees of freedom (numerator, denominator); F, F-value.

Irrespective of the study site and duration of the drought period there was a species specific effect on relative canopy foliage temperatures with *A. pseudoplatanus*, *F. sylvatica* and *T. platyphyllos* being warmer than *F. excelsior*, *P. avium* and *Q. petraea* right from the beginning (Fig. 3). The mean difference between the two groups of tree species was larger at the 'dry' sites ( $1.35 \pm 0.12$  K; mean  $\pm$  se) than at the 'moist' sites ( $0.7 \pm 0.17$  K). At both 'dry' sites the relative canopy foliage temperature of all species strongly increased with prolonged drought, while on the 'moist' sites the canopy warming was less pronounced or even not significant (Hofstetten-Flüh; Fig. 3).

The linear mixed effects model showed a significant overall effect of 'water availability' ('moist', 'dry'), 'duration of the drought period' and 'tree species' on relative canopy foliage temperature as well as significant interaction (Table 3). There was no differences in  $\Delta T_{C-A}$  between 'moist' and 'dry' sites early in the drought period both at Hofstetten-Flüh and at Münchenstein indicating no initial difference between the sites, and also no significant initial difference in vpd sensitivity (Fig. 4). Towards the end of the drought period (22 days) the  $\Delta T_{C-A}$  at the 'dry' sites were significantly ( $P<0.001$ ) larger than at the 'moist' sites (Fig. 4) which explains the significant interaction of 'water availability'  $\times$  'drought' (Table 3). The significant interaction of 'drought'  $\times$  'species' was only caused by *A. pseudoplatanus* which showed a species specific reaction of  $\Delta T_{C-A}$  with the progression of drought. The other 5 species showed similar or site specific canopy foliage warming as drought proceeded (Fig. 4). When *A. pseudoplatanus* was excluded from the analysis, the interaction of 'water availability'  $\times$  'species', as well as the three-fold interaction, lost significance. Using the maximum canopy foliage temperatures instead of the mean canopy foliage temperatures gave the same results but led to larger leaf minus air temperature differences. Analyses of the minimum canopy foliage temperatures showed no differences between species and no clear species specific trends with prolonged drought.

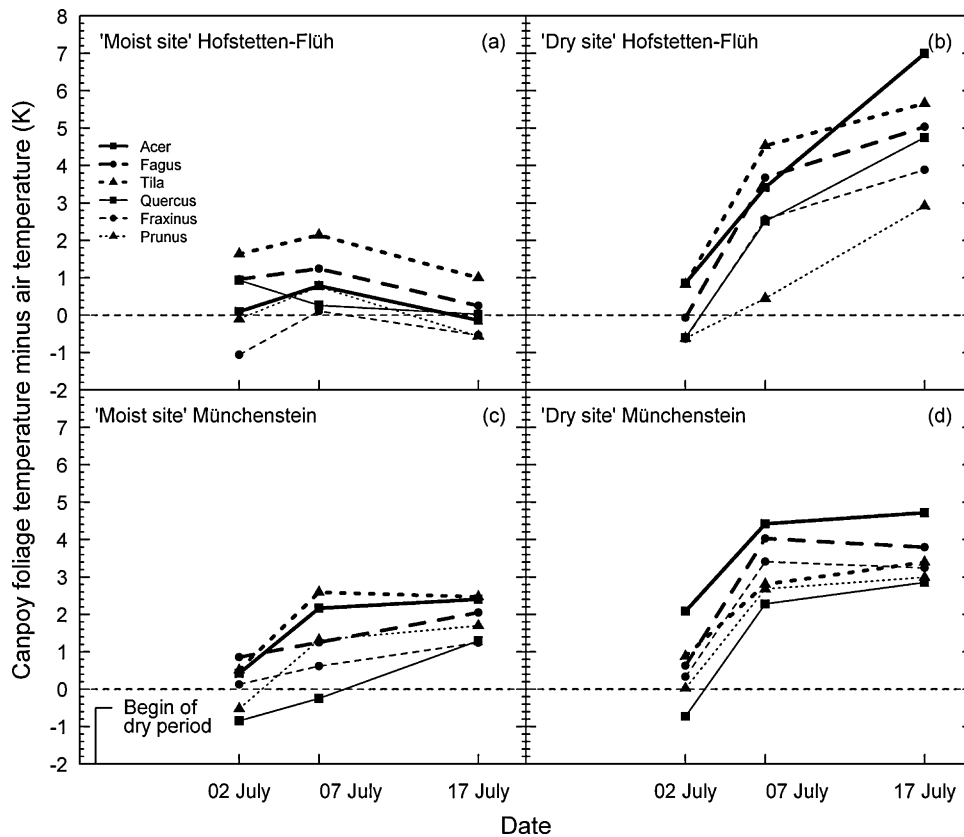
### 3.3. Sap flow measurements

Early during the drought (7 July) the relative sap flow at the 'moist' and 'dry' sites was similar for all species ( $P>0.1$ ) except for *T. platyphyllos* ( $P<0.05$ ) with a significantly lower sap flow at the two 'dry' sites right from the beginning (Fig. 5). After 22 days

**Table 2**

Relative canopy foliage temperatures ( $\Delta T_{C-A}$ ) after 7, 13 and 22 days of drought for all four study sites.

Study site	Relative differences in canopy foliage temperature during the drought period (K)		
	7 days	13 days	22 days
Hofstetten-Flüh			
'Moist site'	0.5	1.1	0.2
'Dry site'	-0.1	3.2	5.0
Münchenstein			
'Moist site'	0.3	1.4	1.9
'Dry site'	0.7	3.6	3.5



**Fig. 3.** Mean relative canopy foliage temperature ( $\Delta T_{C-A}$ ) for *A. pseudoplatanus* (Acer), *F. sylvatica* (Fagus), *T. platyphyllos* (Tila), *Q. petraea* (Quercus), *F. excelsior* (Fraxinus) and *P. avium* (Prunus) during the three thermal imaging campaigns (02 July, 07 July and 17 July). (a and c) Represent the two 'moist' sites and (b and d) the two 'dry' sites. Bold lines indicate the tree species with 'dense canopies' and the fine lines 'open canopies'.

of drought the 'dry' sites had a significantly lower mean sap flux ( $P < 0.001$ , Fig. 5) than the 'moist sites'. The 'moist' sites showed no reduction in relative sap flow after 22 days of drought ( $-0.3 \pm 3.1\%$ , mean  $\pm$  se;  $P = 0.93$ ) except *A. pseudoplatanus* which showed a significant reduction of sap flow with ongoing drought ( $P < 0.05$ ). At the 'dry' sites we observed a strong overall reduction in mean sap flow after 22 days of drought  $-16.4 \pm 5.4\%$  ( $P < 0.001$ , Fig. 5). At the 'dry' sites *A. pseudoplatanus*, *F. sylvatica*, *T. platyphyllos* and *P. avium* showed a stronger reduction in sap flow compared to the 'moist' sites as well as compared to early in the drought period (Fig. 5). *Q. petraea* and *F. excelsior* were not affected by the 22 days of drought (no reduction of sap flow) and showed no differences between 'dry' and 'moist' sites (Fig. 5). However, on such hot, days with clear sky, when vpd was high, *Q. petraea* and *F. excelsior* had somewhat lower rates of sap flow compared to the other species even at the beginning of the drought period with high soil moisture (Fig. 5).

**Table 3**

Linear mixed-effects model results on the effects of water availability ('dry', 'moist' site), duration of the drought period and species identity on relative canopy foliage temperature ( $\Delta T_{C-A}$ ).

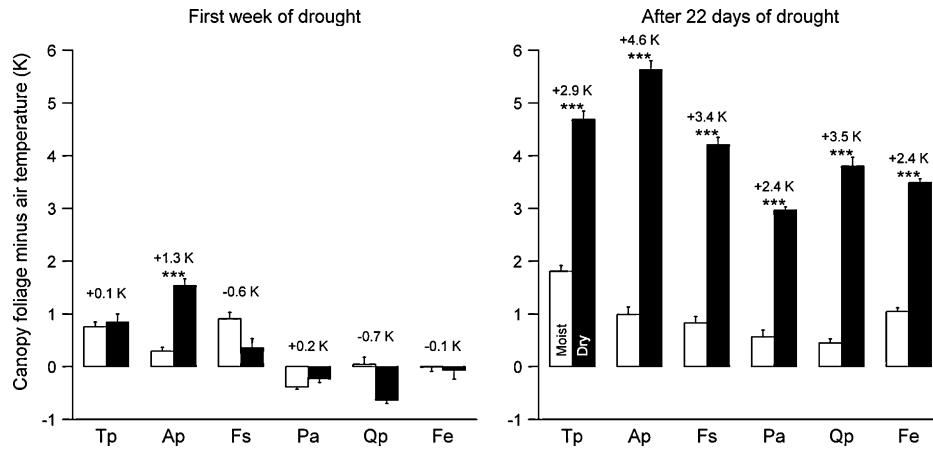
Factor	Df	F	P
Water	1, 177	121.9	<0.001
Drought	2, 220	234.3	<0.001
Species	5, 177	11.0	<0.001
Water $\times$ drought	2, 220	114.5	<0.001
Water $\times$ species	5, 177	3.31	0.007
Drought $\times$ species	10, 220	2.56	0.006
Water $\times$ drought $\times$ species	10, 220	2.50	0.008

Df, degrees of freedom (numerator, denominator); F, F-value.

## 4. Discussion

### 4.1. Species specific canopy foliage temperatures

Our results showed constant differences among tree species, with *A. pseudoplatanus*, *F. sylvatica* and *T. platyphyllos* having higher relative canopy foliage temperatures than *F. excelsior*, *P. avium* and *Q. petraea*. As these differences in  $\Delta T_{C-A}$  were consistent across all sites and thermal imaging campaigns, canopy architecture and leaf morphology are the most likely explanations. The findings that 'dense canopies' (*A. pseudoplatanus*, *F. sylvatica*, *T. platyphyllos*) are warmer than 'open canopies' (*P. avium*, *Q. petraea*) or pinnate leaves (*F. excelsior*) is in line with earlier studies of canopy foliage temperatures in a mature temperate forest (Leuzinger and Körner, 2007a) and trees in urban environments (Leuzinger et al., 2010). On clear sky days with high soil moisture Leuzinger and Körner (2007a) found  $\Delta T_{C-A}$  of 0.3–2.7 K for 'open canopies' and 4.5–5 K for 'dense canopies' while we recorded lower  $\Delta T_{C-A}$  with  $-0.4$  to 0.1 K for 'open canopies' and 0.6–0.8 K for 'dense canopies' at the beginning of the drought period. The lower  $\Delta T_{C-A}$  found in our study can be explained by the coarser spatial resolution as we flew ca. 100 m above the canopy whereas the data from Leuzinger and Körner (2007a) was recorded from a crane only 10 m above the canopy. The resolution of our data (ca. 350 cm<sup>2</sup>/pixel) made it impossible to exclude small scale self shading (dm-scale) of branches and leaves often occurring in spatially structured canopies. By including a proportion of self shaded leaves/branches we tend to underestimate the actual leaf temperature of fully sun exposed leaves (as reported by Leuzinger and Körner, 2007a) and therefore rather present a mean canopy foliage temperature. Additionally, our thermal imaging campaigns took place on "heat days" with more than



**Fig. 4.** Relative canopy foliage temperature ( $\Delta T_{C-A}$ ) for *T. platyphyllos* (Tp), *A. pseudoplatanus* (Ap), *F. sylvatica* (Fs), *P. avium* (Pa), *Q. petraea* (Qp) and *F. excelsior* (Fe) with differences between ‘moist’ (white columns) and ‘dry’ sites (filled columns). The left panel shows the pooled data after 7 days of drought and the right panel after 22 days of drought. Error bars represent one standard error. \* $P < 0.05$ , \*\* $P < 0.01$ , and \*\*\* $P < 0.001$ .

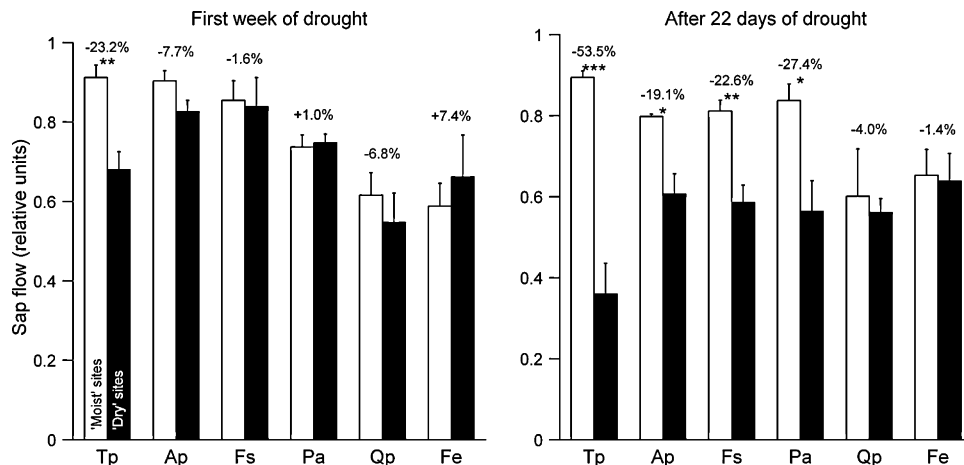
30 °C air temperature, while the studies mentioned before reported about 25 °C air temperature. The higher the air temperature the less pronounced is commonly the radiative heating above the air temperature.

4.2. Monitoring plant water status by thermal imagery

There are many studies available using thermal imagery to monitor plant water status in monocultures of crops (mostly irrigation scheduling; e.g., Clawson and Blad, 1982; Stegman and Soderlund, 1992; Jones, 1999a; Alves and Pereira, 2000; Jones et al., 2002) but few studies working with near-natural forest stands (Leuzinger and Körner, 2007a,b) and, to our knowledge, none with concurrent sap flow data. Our data, thus also demonstrate the power of thermal imagery to detect forest patches first/most affected by drought even in highly diverse mixed forests.

With ongoing drought, the  $\Delta T_{C-A}$  of ‘dry’ and ‘moist’ sites diverged, with higher  $\Delta T_{C-A}$  at ‘dry’ sites (Fig. 4). Unfortunately, the large differences in  $\Delta T_{C-A}$  between ‘moist’ and ‘dry’ sites after 22 days of drought cannot be attributed to the measured differences in soil water potential, given we had no information on soil water availability in greater soil depths. Yet, at all sites marked shrinkage cracks indicated severe desiccation in the upper soil horizon which was corroborated by readings of the soil matrix potential probes

that reached their detection limit (–500 kPa, Fig. 2). Consequently, the tree-effective differences must have occurred deeper in the rooted soil profile, inaccessible at three of the four sites because of rocks and gravel. Since there were no site-specific differences early in rainless period, when soils were still moist, we can exclude an initial bias (Fig. 3). It is well known that hardwood tree species have a maximum rooting depth >10 m (Jackson et al., 1996; Schulze et al., 1996; Schenk and Jackson, 2002), too deep to take any readings. Indicator species at the forest floor (Landolt, 1977) clearly evidenced strong contrasts in long-term water availability in the upper soil profile at the study sites but cannot provide information on water availability in deeper soil horizons. The lower water availability at the ‘dry’ sites was also reflected in higher canopy vpd (Fig. 2). Köcher et al. (2009) showed that both, low soil water potential and high vpd reduce leaf conductance in five deciduous hardwood tree species. Changes in transpiration (latent heat flux) are directly coupled to leaf temperature (Leinonen et al., 2006; Guillioni et al., 2008) and therefore, an increase in canopy foliage temperature at otherwise similar environmental conditions (solar radiation, wind), indicates reduced transpiration (Jones, 1999b). We conclude that high relative canopy foliage temperatures are an indication for forest patches first affected during a drought period. Anecdotal visual evidence from local foresters supports this hypothesis, because trees on our ‘dry’ sites suffered more severely



**Fig. 5.** Sap flow (relative units) of *T. platyphyllos* (Tp), *A. pseudoplatanus* (Ap), *F. sylvatica* (Fs), *P. avium* (Pa), *Q. petraea* (Qp) and *F. excelsior* (Fe) with percent differences between ‘moist’ (white columns) and ‘dry’ sites (filled columns). The left panel shows the pooled data after 7 days of drought and the right panel after 22 days of drought. Error bars represent one standard error. For each species we had four trees at ‘moist’ and ‘dry’ sites (48 trees in total). \*\*\* $P < 0.001$ .

from the exceptionally dry and hot summer 2003 than trees growing at the 'moist' sites. Although this campaign did not cover such an extreme drought event in 2010, the sap flow data prove that the higher relative canopy foliage temperatures at the 'dry' sites were due to a reduction in transpiration as the sap flow was significantly lower at the 'dry' sites at otherwise similar solar radiation and wind speed (Fig. 5).

At a larger scale, the differences in mean relative canopy foliage temperature between forest sites could also be a result of different abundances of species with inherently "hotter" canopies. However, in our case all species were present at all sites, and the sites with the lowest  $\Delta T_{C-A}$  ('moist' sites) had, in fact, a considerably higher proportion of 'dense canopy' species especially *A. pseudoplatanus* and *T. platyphyllos* that had been shown to collect more heat. One could, thus, invert the argument and attribute their greater abundance at the more humid sites to their overheating-sensitive canopies.

#### 4.3. Drought sensitivity ranking of tree species

In terms of relative canopy foliage temperature all studied tree species (except *A. pseudoplatanus*) showed similar responses to drought. The more pronounced canopy foliage heating of *A. pseudoplatanus* is likely the result of generally low stomatal conductance and high leaf water potential even at noon (Köcher et al., 2009; Leuzinger et al., 2010) leading to low evapotranspirative cooling. *A. pseudoplatanus* is known as a drought avoiding species (Khalil and Grace, 1992; Lemoine et al., 2001) exerting pronounced feed forward responses of stomata to low air humidity (Körner, 1985). In fact, *A. pseudoplatanus* was the only species showing a reduction in sap flow at the 'moist' sites while all other species showed no reduction of sap flow at the two 'moist' sites even after 22 days of drought.

The lack of additional species specific responses of  $\Delta T_{C-A}$  might be explained by several factors. First the drought period reported in this study (max. 22 days), is not exceptional for Switzerland and did not induce severe water stress to the trees. A more severe drought, such as in 2003, might lead to more diverging relative canopy foliage temperatures as plant species specific regulations of leaf conductance and sap flow take place (Leuzinger et al., 2005). Second the large heterogeneity among trees of the same species (age, size, shape, micro-site, etc.) makes it difficult to detect species specific changes in stomatal conductance as a 10% reduction results in less than 0.4K canopy foliage warming (for calculations see Jones, 1992). Yet, there is a clear separation between 'dense canopy' species (*A. pseudoplatanus*, *F. sylvatica*, and *T. platyphyllos*) and 'open canopy' species (*P. avium*, *Q. petraea* and *F. excelsior*) at the 'dry' compared to the 'moist' sites, which might indicate that the 'close canopy' species are more affected by drought.

The sap flow revealed a clear difference between the two ring-porous species *Q. petraea* and *F. excelsior* and the other four, diffuse-porous species at the 'dry' sites. While *A. pseudoplatanus*, *F. sylvatica*, *P. avium* and *T. platyphyllos* had strongly reduced sap flow with increasing drought, the sap flow of *Q. petraea* and *F. excelsior* stayed constant at a somewhat lower rate. The generally lower relative sap flow in these two species at even high soil moisture might reflect an ecological trade-off. On hot and sunny days (high vpd) *Q. petraea* and *F. excelsior* seemed to down regulate their sap flow independent of water availability while the other studied species transpired at very high rates. This might reflect a safety measure against cavitation, given the wide vessel diameters in these ring-porous species (*F. excelsior* and *Q. petraea*). Such down regulation might also contribute to water savings at greater soil depth in those deep-rooted species, explaining their robustness against even severe drought (Leuzinger et al., 2005).

Based on the relative canopy foliage temperature and sap flow data we considered *A. pseudoplatanus* as the most drought sensitive

species followed by *T. platyphyllos*, *F. sylvatica* and *P. avium*. The two most drought tolerant species are clearly *F. excelsior* and *Q. petraea*. Our drought sensitivity 'ranking' is supported by measurements of leaf conductance, xylem sap flow and leaf water potential of five temperature broad-leaved tree species with *A. pseudoplatanus* and *F. sylvatica* being the most drought sensitive and *F. excelsior* the most drought tolerant species (Köcher et al., 2009).

However, we only documented short-term responses of trees to summer drought by reduced transpiration via stomatal regulation. In case of repeated drought events, long-term adaptations such as growing deeper roots and reductions in leaf area are likely in most tree species (Sperry et al., 2002; McDowell et al., 2008). In addition to the control of water status in adult trees by tree density (LAI), the longer-term drought impact on recruitment/early life stage needs to be explored as well. Another avenue, dendroecological analysis, offers insight into the longer-term growth responses and the impacts of past extreme events that will be reported in a forthcoming study. The difficulty with tree rings is that their width only reflects the periods during which they are formed (early season), while drought later in the season may severely impact trees, without (or with great delay) producing a tree ring signal (Cook and Kairiukstis, 1990). Airborne digital infrared thermometry is a trustworthy tool that permits large-scale screening of the species specific response to drought, but species such as *A. pseudoplatanus* will warm, despite high soil moisture and, thus, a 'warm canopy' is not necessarily an indication of poor water supply, but may simply reflect concurrent transpiration.

Nevertheless, *F. excelsior* and *Q. petraea* are known to be drought-tolerant and to have large distribution ranges including continental Eastern Europe (Ellenberg, 2010). In contrast, the drought-sensitive *A. pseudoplatanus*, *F. sylvatica* and *T. platyphyllos* are mostly restricted to sub-oceanic Central and Western Europe (Ellenberg, 2010). Not only at the European scale but also at a regional scale we see shifts in tree species composition along small scale moisture gradients with lower abundance of *A. pseudoplatanus*, *F. sylvatica* and *T. platyphyllos* at drier micro-sites and an increase of *F. excelsior* and *Q. petraea* (personal observations and species abundance on study sites; Marigo et al., 2000).

## 5. Conclusion

Our process based analysis of the drought sensitivity of six major European deciduous tree species revealed clear species and micro-site specific responses with *F. excelsior* and *Q. petraea* being the most drought tolerant species in terms of maintenance of transpirational flux followed by *P. avium* and *F. sylvatica* and the two most drought sensitive species *T. platyphyllos* and *A. pseudoplatanus*. Providing the first combined evidence for canopy responses, sap flux and soil moisture, this ranking reflects the drought sensitivity of tree water relations and does not hint at stress physiological impacts/sensitivity under deleterious drought. Because such restrictions of water relations will feed back on overall tree performance, these different sensitivities could translate into a change in competitive abilities in favour of more drought tolerant tree species. In the medium-term, we therefore expect *F. excelsior* and *Q. petraea* to profit at least at drier micro-sites. Since both, tree species identity and local soil conditions had strong effects on the drought responses, the interaction of species with water availability should be incorporated in competition based community models. Given these species specific responses to water shortage, species abundance is important in catchment based hydrological models. Our results have immediate implications for forest planning in dry regions or those areas that are likely to become drier in a warmer future.

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