



Tree species from two contrasting habitats for use in harsh urban environments respond differently to extreme drought

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Abstract

The role of trees in city cooling has warranted much attention based on concerns over climate change and urban expansion. Simultaneously, there is an interest in introducing species from dry habitats to cope with the increasing risks of drought under climate change. The general understanding is that the evolutionary adaptation to respective resource supplies in species' habitats affects their environmental tolerance. The physical performances of six frequently planted species, originating from two contrasting habitats, were tested in a drought experiment. We (1) investigated if species from drier habitats are more drought tolerant than species that have evolved in Central European woodlands under a temperate climate regime and (2) discussed the effect of tolerance on the cooling potential of these trees. Native species from mesic habitats maintained only 48% of their controls sap flux and of these species, *Tilia cordata* had the worst performance with premature leaf senescence. Species from drier habitats had less reduction in sap flux (60%) but lower stem growth, possibly favouring (fine) root development into deeper soil layers, as observed when comparing linden species. Higher stem water exploitation and stronger regulation of water use at high evaporative demand were further reaction patterns that likely helped species from dry habitats maintain good physiological functions. Therefore, even under sustained drought, we expect them to have a higher cooling capacity. As a conclusion, they should be favoured for planting in extreme urban environments. Systematic screening and testing of promising species from target habitats is recommended to diversify the choice of species.

Keywords Climate change · Cooling effects · Drought tolerance · Sap flux density · Resistance · Urban trees

Introduction

Urban greenery is a crucial factor for creating thermal comfort in urban areas because heat loads caused by densely built structures can be reduced via evapotranspiration and shading (Shashua-Bar and Hoffmann 2000; Armson 2012; Gillner

et al. 2015; Rahman et al. 2017b). This effect will become increasingly important when heat waves will become more frequent and intense under climate change with adverse impacts on human health (e.g. Endlicher et al. 2008). The magnitude of the cooling effect of trees depends on their size and leaf amount (Peters et al. 2010; Armson 2012; Armson et al. 2012; Gillner et al. 2015) as well as on their constitution under the prevalent growing conditions and resource supplies (Rahman et al. 2017a).

Under a changing climate, drought may prove to be a critical constraint for vegetation in urban areas (Gill et al. 2007) and, in particular, at roadsides and highly paved squares (Moser et al. 2017; Rahman et al. 2017a). Here, tree species, which have evolved in Central European woodlands under a temperate climate regime, are increasingly reaching their limits of plasticity (Roloff 2013). Consequently, there are recently many experimental studies testing more drought-adapted but less frequently planted tree species and cultivars (e.g. Fini et al. 2009; Hiemstra 2011; Sjöman et al. 2012; GALK 2018; LWG 2018) as well as theoretical assessments aiming to identify species sensitivities based on knowledge about the environmental

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conditions in the natural habitats (Duhme and Pauleit 2000; McCarthy et al. 2011; Sjöman et al. 2012; Roloff 2013). For the future harsh and challenging urban conditions, specific traits of plants that are exposed to water scarcity in their natural habitats may be suitable. Studies show that species growing in areas of low rainfall or seasonal drought tend to have greater water-use efficiency at the leaf and tree scales (McCarthy et al. 2011; Stratopoulos et al. 2018) and a higher tolerance to negative water potential (Klein 2014) or embolism resistance, respectively (Choat et al. 2012), in comparison to species from wetter habitats. In addition, there are specific morphological characteristics that have evolved to allow survival in regions with limited resource supplies, such as hairy, thick leaves or extensive root systems (Larcher 2001; Roloff et al. 2013).

Climate change is increasing the need to improve our understanding of tree function under water limitations. However, the recent research knowledge on urban tree species tolerance to drought, which is based on experiments, is still limited (Fini et al. 2009; Moser et al. 2017; Rahman et al. 2017a). Therefore, we performed a comparative study of six frequently planted tree species and cultivars, which originated from two contrasting habitats in terms of water availability. The study provides data of the water use determined by continuous sap flux measurements at the stem level, fine root and stem growth as well as phenology during a soil drying experiment of a complete growing cycle in 2017. We (1) investigated if species from drier habitats are more drought tolerant than species that have evolved in Central European woodlands under a temperate climate regime and (2) discussed the effect of tolerance on the cooling potential of these trees.

Material and methods

Study site, species selection and drought experiment

The experimental site (48° 08' 05" N, 11° 28' 47" E, 534 m a.s.l.) is located in the southwest of Munich, Germany. Long-term (1981–2010) annual means of the temperature and rainfall from the nearest weather station in the city centre of Munich are 9.7 °C and 944 mm, respectively (DWD 2018). The municipal nursery is characterised by an almost uniform topography and likely small microclimatic variations. The predominant soil types range from moderate sandy loam to strong loamy sand, as estimated by a finger test.

Six to eight individuals each of the following deciduous and diffuse porous species and cultivars of the stem circumference size class 16–20 cm were selected: *Acer platanoides* L., *Carpinus betulus* L. 'Fastigiata' and *Tilia cordata* Mill. 'Greenspire', which are frequently planted native species/cultivars with presumably less drought tolerance, and *Acer campestre* L. *subsp. campestre*, *Ostrya carpinifolia* Scop. and *T. tomentosa* Moench 'Brabant' originating from drier

habitats, which appear suitable for future plantings in current street tree trials and scientific field experiments (Fini et al. 2009; Hiemstra 2011; GALK 2018; LWG 2018). In addition, there is a range of shade tolerance between the study species (Niinemets and Valladares 2006; Table 1).

For simplicity, we will refer to all species and cultivars as 'species' and use the abbreviations listed in Table 1. Because we compared tree species naturally occurring in native habitats with relatively higher and lower water availability, we use the terms high- (HR) and low-resource (LR) species (Chapin III et al. 1993).

We employed an experimental setting where we simulated the conditions of an enduring drought event to investigate the physiological and growth responses of the trees. In May 2017, we installed waterproof, translucent tarpaulins (2 m × 3 m) in the middle row of 50% of the individuals ('dry') at a height of 1 m, sloping to the ground in the north and south directions 3 m from the trees. The tent-like constructions prevented rain infiltration close to the tree stems. A second group with the same number of individuals per species was exposed to the prevailing weather conditions and served as a control ('con') (Fig. 1). Each plot was made up of three to four plants per species and treatment, which were all planted in spring 2014 in parallel rows at 2 m × 3 m spacing at two separate fields (field A and B; Table 1). In the case of *Ac*, *Cb* and *Oc*, the replicates for the drought experiment were planted in one row, whereby the dry treatment and the control plants were kept at distance by at least one unmeasured tree between them. In the case of both *Tilia* species and *Ap* the individuals were spread over at least two planting rows.

Climate and soil moisture measurements

The photosynthetically active radiation ($\mu\text{mol m}^{-2} \text{s}^{-1}$; PAR; LI-190; LI-COR Biosciences, Lincoln, USA) was recorded at field B on top of a data logger cupboard. A full suite of climatic variables were sampled every 10 min with a weather station (Davis Vantage Pro2; Davis Instruments, Hayward, USA) placed in an unshaded field approximately 200 m from the experiment. Due to inaccurate readings, precipitation data were also obtained from the nearest weather station from the German Weather Service (DWD) at the Munich City Centre. The vapour pressure deficit (hPa; VPD) was computed from air temperature and humidity data and normalised for daytime (D_z) as introduced by Ewers et al. (2001).

The volumetric soil water content (%; VWC) was measured using HS-10 sensors (Decagon Devices, Pullman, USA) inserted horizontally at a depth of 30 cm in the A-horizon located 40 cm from the tree stems. For each species and treatment, one sensor was used for one centrally located individual in the row. Like for all the other recorded parameters, that we will refer to hereinafter, 10-min means were calculated from 1-min readings and logged (field A: CR800

Table 1 Characteristics and biogeographical information of the surveyed trees. Diameter at breast height (DBH) is given for May before the drought experiment started

	Code	Field	Native throughout ¹	DBH [cm ± sd]	Shade tolerance ²	Drought tolerance ²
1 Commonly planted species/cultivars from species-rich forests and woodlands ¹ (HR)						
<i>Acer platanoides</i>	Ap	B	EUR (except British Islands), Caucasus	5.66 ± 0.18	4.20 ± 0.37	2.73 ± 0.16
<i>Carpinus betulus</i> 'Fastigiata'	Cb	A	EUR, Caucasus, asian Turkey, Iran	5.43 ± 0.22	3.97 ± 0.12	2.66 ± 0.16
<i>Tilia cordata</i> 'Greenspire'	Tc	A	EUR, Caucasus, N-Iran, W-Siberia	5.95 ± 0.16	4.18 ± 0.16	2.75 ± 0.15
2 Promising species/cultivars from wooded steppes and dry forests ¹ (LR)						
<i>Acer campestre</i>	Ac	A	EUR, Caucasus, asian Turkey, N-Iran Morocco, Algeria	5.63 ± 0.12	3.18 ± 0.14	2.93 ± 0.32
<i>Ostrya carpinifolia</i>	Oc	B	EUR: France, Apennine, Switzerland, Austria, Hungary, Balkan, asian Turkey, Syria, Caucasus	5.93 ± 0.21	3.94 ± 0.18	3.07 ± 0.17
<i>Tilia tomentosa</i> 'Brabant'	Tt	B	EUR: Balkans, eastern part of Central EUR, asian Turkey, Syria	6.57 ± 0.14	3.34 ± 0.34	2.81 ± 0.12

¹ According to Kiermeier (1995) and Roloff and Bärtels (2006)

² According to Niinemets and Valladares (2006) (Appendix A). Tolerance scales range from 0 (no tolerance) to 5 (maximal tolerance)

connected to an AM16/32 B multiplexer, Campbell Scientific, Logan, UT, USA; field B: Agilent 34970A Data Acquisition/Switch Unit, Agilent Technologies, Santa Clara, CA, USA). Because the continuous measurement devices failed many times probably due to high soil compaction and drying, we additionally used a portable soil moisture meter (UMP-1, UGT, Müncheberg, Germany) for point measurements in the upper 10 cm of the soil during 4 days in the summer. The readings were made at defined distances from all study trees (Fig. 1).

Spring and autumn phenology

We classified the spring and autumn phenology according to the BBCH phenological growth stages and identification keys (BBCH 2001). The phenological development stages were recorded once or twice a week between the end of March (beginning of bud swelling, BBCH 01) and the middle of May and between the beginning of October and the end of November. In addition, we made observations concerning early wilting throughout the summer.

Stem growth and fine root development

From April to November 2017, we measured the diameter of the trees at a height of 1 m at the start of each month using a digital calliper. Measurements in two perpendicular directions (N–S and E–W) were performed and averaged. On respectively three individuals at both dry and control plots of the two *Tilia* species, we additionally installed a total of 12 high-resolution electronic dendrometers (DDL, Ecomatik, Dachau, Germany) at a height of 1.3 m.

Fine root development for both *Tilia* species under dry treatment and control conditions in May (pre-drought),

September and November 2017 was analysed with the help of soil cores. A pre-test campaign revealed that the distribution pattern of the root systems was similar to a cylinder with a diameter of around 70 cm and a height of around 35 cm. In every coring campaign, four soil cores were sampled for each individual tree to a depth of 30 cm with a soil auger (3 cm in diameter), for the 0–10-cm, 10–20-cm and 20–30-cm layers, two of which were located at a distance of 15 cm and the other two were located at a distance of 30 cm from the trunk. Finally, fine roots (< 2 cm) were filtered using sieves, washed, dried and weighed to estimate the dry weight.

Stem xylem flux

We measured sap flux density (g H₂O cm sapwood⁻² min⁻¹; J_S) in the outer 20 mm of the xylem with Granier-type sensors (Granier 1987); all trees were equipped with pairs of a control and a continuously heated downstream probe (SF-G & CCS, Ecomatik, Dachau, Germany). On the north side of the stems, the sensors were inserted radially into the xylem at or near a height of 1.8 m and 8 cm apart. Granier's empirical equation (1987) was used, to convert the voltage values into volumetric sap flux densities:

$$J_s = 0.714 \left[\frac{\Delta T_{max} - \Delta T}{\Delta T} \right]^{1.231} \quad (1)$$

where ΔT indicates the temperature difference between the sensor needles and ΔT_{max} indicates the maximum ΔT between the sensor needles within a 24-h interval (equals no J_S). In this young age of the trees, the entire cross-section of the trunks was assumed to be hydro-active with a uniform J_S rate across the entire sapwood depth.

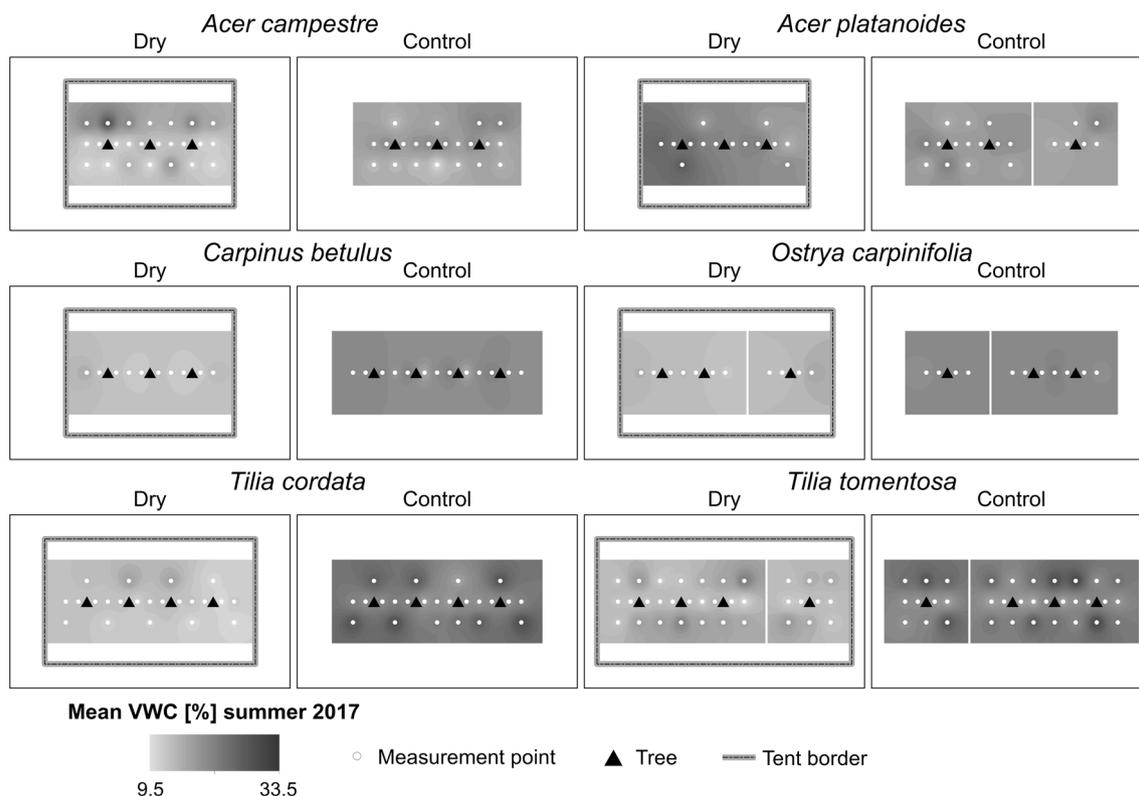


Fig. 1 Interpolation maps (inverse distance weighted) of the volumetric soil water contents (%; VWC) at a soil depth of 10 cm averaged over four measurement days in summer 2017 and collected at defined distances from the study trees. The rooting zones of the individuals in the

respective left species graphics were covered by the rain-out constructions ('dry'), whereas the individuals in the right images belonged to the control group

Statistical analysis

To evaluate simultaneously the effect of the two grouping variables treatment and species on J_S and stem growth, we used a two-way analysis of variance (ANOVA) for unbalanced designs with each tree assumed to be an independent replicate. The resistance to drought was quantified as the ratio between the physiological performance during the drought and that under normal conditions, as represented by the control plants (Kunz et al. 2016). Statistical analysis of fine root data for both *Tilia* species was performed using a one-way ANOVA and Tukey's post hoc test. In addition, the response types and strengths of the J_S to the atmospheric drivers PAR and D_Z were examined by developing exponential saturation models (Peters et al. 2010) in the form of $y = a(1 - \exp(-bx))$, where a and b are fitting parameters, and simple linear models. The response of J_S to mean daily VWC was investigated using Spearman's nonparametric measure of rank correlation. For all statistical analyses and creating of most of the graphics the software package R, version 3.2.1 (R Core Team 2014) was used. Measurements of VWC in 10 cm soil depth were processed and visualised with the help of ArcGIS, version 10.2.1 (Esri 2014; Fig. 1). To create a map from the discrete data, we compared the results of different interpolation

algorithms provided by the software. The inverse distance weighted (IDW) method was selected as the most appropriate approach evaluated by visual inspection.

Results

Environmental conditions

The winter of 2016/17 was mild, and the spring was considerably warm, sunny and dry. After a strong return to cold weather in April, there were midsummer-like temperatures measured towards the end of May. June was also exceptionally warm, dry and sunny with D_Z values of more than 30 (Fig. 2) after strong precipitation events that occurred at the beginning of the month. July and August, however, were characterised by heavy rainfall alternating with high sunshine levels. September and the first half of October were cold, rainy and considerably cloudy. The second half of October was summerlike again. Snow and night frosts started in the middle of November (DWD 2018).

An analysis of the soil moisture data confirmed a high correlation ($r_S = 0.70$) between the measurements at 10 cm and 30 cm with the VWC being on average 5.8% higher in the deeper soil layer. Averaged for the whole experiment, the

dry treatment plots had significantly lower soil moisture contents ($P < 0.001$) at a soil depth of 30 cm in comparison to the control plots, with the roofed *Tt* showing the lowest average value of 19.36%. Therefore, the data indicated the overall success of the soil drying experiment. In addition, we found that the VWC 1 m from the trees, and therefore closer to the tent border, was significantly higher than that in the centre of the roofs ($P = 0.014$). At the plot of *Ap*-dry, however, there were disproportionately high moisture contents probably because of soil compaction. The VWC values in the 30-cm layer were the highest of all groups with on average 31.87% and a maximum of 49.99%. Therefore, the difference VWC between the treatments was not significant for this comparison pair.

Leaf phenology

The phenological timing in spring among the different tree species spread over several weeks (Fig. 2). For the majority of the individuals, completion of leaf expansion (BBCH 19) was observed between the second and third week of May. The

fastest developing species was *Tc*, which unfolded its leaves 1 week earlier than the average (day of year (DOY) 127). The slowest developing species were *Oc* and *Tt*, which did not unfold their leaves until the third week of May (DOY 139).

In autumn, there was higher variability between the species and treatments. Individuals of *Tc*-dry were leafless (BBCH 97) in the middle of October but leaf discoloration (BBCH 92) was already observed in July. *Oc* and *Tt* had long vegetation periods; however, the effect of drought was clearly visible as well. In the control group, especially *Oc* maintained green, healthy foliage far into November (not shown in the graph), whereas in the dry treatment, leaf discoloring appeared approximately 1 month before. On average, the drought caused no difference in the timing of autumn phenology in *Ap* and *Cb* and *Ac* kept its foliage even longer.

Sap flux

The differences in leaf phenology, which were perceived visually, were also reflected in the differences in water consumption (Fig. 2). *Tc* and *Oc*, which had the biggest timing

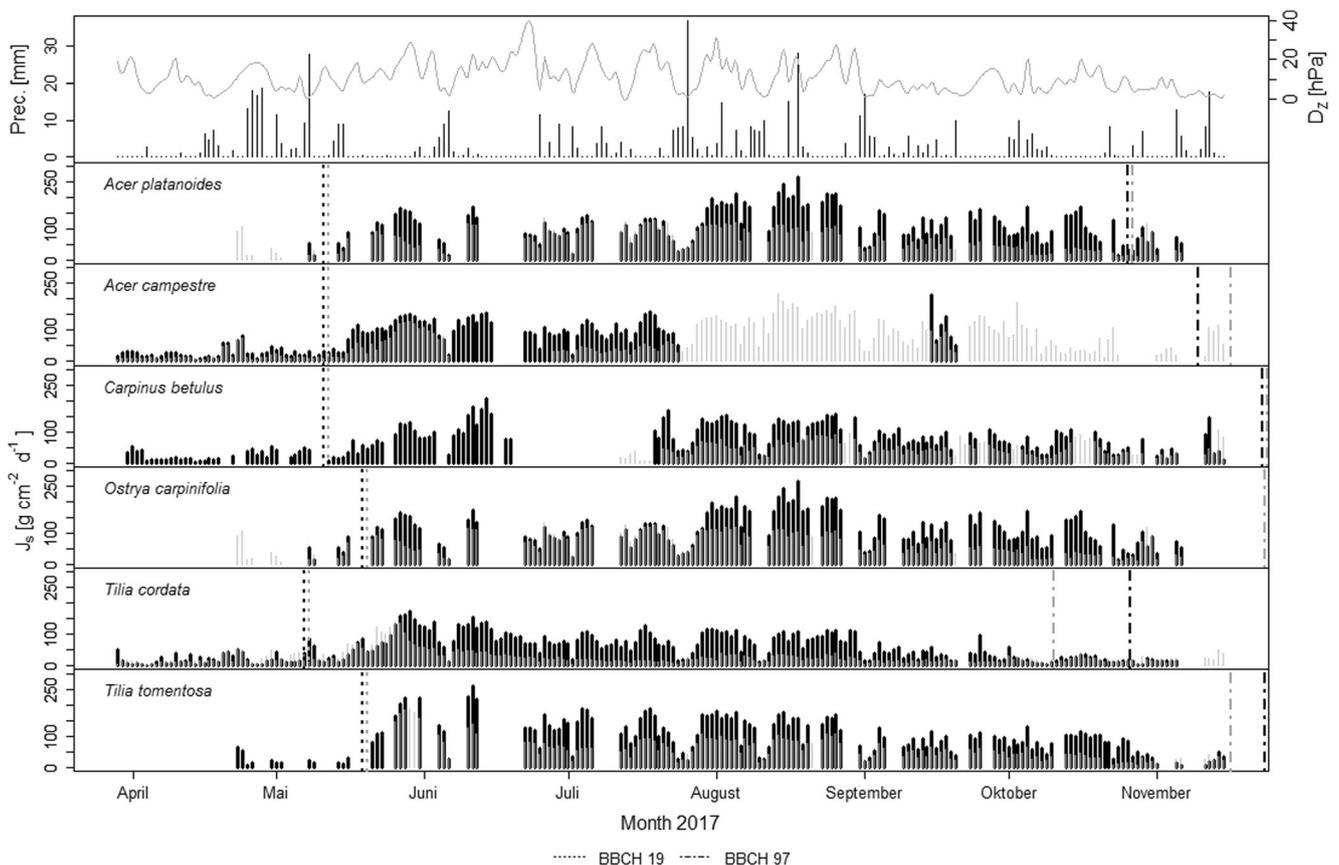


Fig. 2 Daily amounts of precipitation (mm) and the vapour pressure deficit normalised for day length (D_z) for the entire study period in 2017, as well as the sap flux density (J_s) for the six species under the dry treatment (transparent grey) and control (black) conditions. Each panel represents the mean of all the trees per species and treatment. The

vertical lines mark dates for the completion of leaf folding (BBCH 19) and leaf-fall (BBCH 97). Missing data corresponds to days when the equipment failed. Gaps in the meteorological data were replaced with data from the German Weather Service (DWD; available online) measured in the Munich City Centre

differences in leaf-fall and discolouring between the treatments, also showed the strongest impact of drought on J_S . Between June and September, dried out *Oc* and *Tc* had only 50% and 33% of their control J_S levels, respectively (Table 2). July was the most critical month for *Tc*-dry with approximately 20% J_S of the control (Figs. 2 and 3). *Ap* and *Ac*, whose leaf-fall was not (negatively) affected by the dry treatment, also showed a smaller impact on the J_S (63% and 73%, respectively). *Cb*-dry and *Tt*-dry reached percentages of 58% and 57%, respectively. Overall, species and treatment highly affected the J_S ($P < 0.001$).

In Fig. 3, where we depicted the *Tilia* data for the diurnal trends, it can be seen that generally, J_S was highest during the radiation-intensive and hottest hours of the day (between 1220 and 1430 h). All dried out trees, however, had also the strongest reduction in J_S during this time, as well as often a delayed morning increase and an earlier afternoon decrease, in comparison to the control.

Diurnal stem variation, annual growth and fine root development

Figure 3 shows the negative correlation between the daily J_S and the stem diameters due to depletion and replenishment of stem-stored water. The highest diameter changes were observed during the exceptionally warm June period and

gradually decreased towards autumn for both species. In general, they were higher for *Tt* than for *Tc*, which could be due to their thicker stem diameters or bark parenchyma, respectively (Table 1). For *Tc*, the differences between both treatments were on average smaller. In the dry June and in July, *Tc*-con showed higher shrinkages in the course of the day in comparison to *Tc*-dry. For *Tt*-con, however, the reverse was the case. In June, dried out *Tt*-dry shrunk up to 167.9 μm on average and a single individual even up to 214.5 μm during the day, whereas *Tc*-dry had a maximum variation of only 88.5 μm on average.

Concerning absolute BAI, of the control groups, *Ac* and *Tc* were considerably less productive ($4.08 \pm 3.15 \text{ cm}^2$ and $2.56 \pm 0.38 \text{ cm}^2$, respectively) than *Tt*, which by far has grown most ($8.53 \pm 0.24 \text{ cm}^2$) (Table 2). *Cb*-con had the highest relative BAI ($12.21 \pm 1.74\%$) and was significantly stronger growing than *Tc*-con ($4.57 \pm 0.77\%$). Of the dry treatment, *Ap* reached the highest absolute and relative BAI ($6.44 \pm 2.06 \text{ cm}^2$ and $12.25 \pm 3.25\%$, respectively) and *Oc* and *Tc* in both cases had the lowest values.

Growth was highly different between species ($P < 0.001$), whereas the treatment did not have significant effects. *Ap* showed the highest resistance to drought with even higher stem growth in the dry treatment. *Ac* had the second highest resistance (0.66 for the absolute and 0.69 for the relative BAI), *Tc* and *Tt* exhibited medium resistance, and *Cb* and *Oc* the lowest resistance of growth under drought.

Table 2 Means, standard errors (SE) and resistance with respect to the control (*R*) for the absolute (cm^2) and relative (%) basal area increment (BAI) and the sap flux density. Valid numbers of observations for each species-treatment combination that were used for the two-way-ANOVA

are given as well as the *p*-values of single fixed effects. To exclude data that was recorded during the spring and autumn phenological development and before the start of the rainout installations, we only analysed the sap flux data between June and September

Variable	Species	<i>n</i>		Control		Dry		<i>R</i>	<i>p</i> drought <i>p</i> species
		Con	Dry	Mean	SE	Mean	SE		
Absolute BAI (cm^2)	<i>Ap</i>	3	3	6.12	0.56	6.44	1.19	1.05	0.235
	<i>Ac</i>	3	3	4.08	1.82	2.69	0.48	0.66	< 0.001
	<i>Cb</i>	4	4	5.73	0.45	1.29	2.03	0.22	
	<i>Oc</i>	3	3	5.99	0.45	1.29	0.67	0.22	
	<i>Tc</i>	4	4	2.56	0.19	1.20	0.47	0.47	
	<i>Tt</i>	4	4	8.53	0.12	3.89	0.40	0.46	
Relative BAI (%)	<i>Ap</i>	3	3	11.25	0.83	12.25	1.87	1.09	0.265
	<i>Ac</i>	3	3	7.48	3.18	5.17	0.92	0.69	0.001
	<i>Cb</i>	4	3	12.12	0.87	2.40	4.41	0.20	
	<i>Oc</i>	3	3	10.15	0.38	2.32	1.20	0.23	
	<i>Tc</i>	4	4	4.57	0.38	2.08	0.79	0.46	
	<i>Tt</i>	4	4	11.79	0.37	5.69	0.52	0.48	
Sap flux density ($\text{g cm}^{-2} \text{ d}^{-1}$)	<i>Ap</i>	2	2	125.12	0.33	78.63	4.00	0.63	< 0.001
	<i>Ac</i>	3	2	103.35	10.25	75.50	33.84	0.73	< 0.001
	<i>Cb</i>	2	2	84.36	13.70	48.78	16.58	0.58	
	<i>Oc</i>	2	2	77.61	8.53	38.82	2.39	0.50	
	<i>Tc</i>	3	4	71.15	11.25	23.17	3.34	0.33	
	<i>Tt</i>	3	3	111.65	10.34	63.35	7.44	0.57	

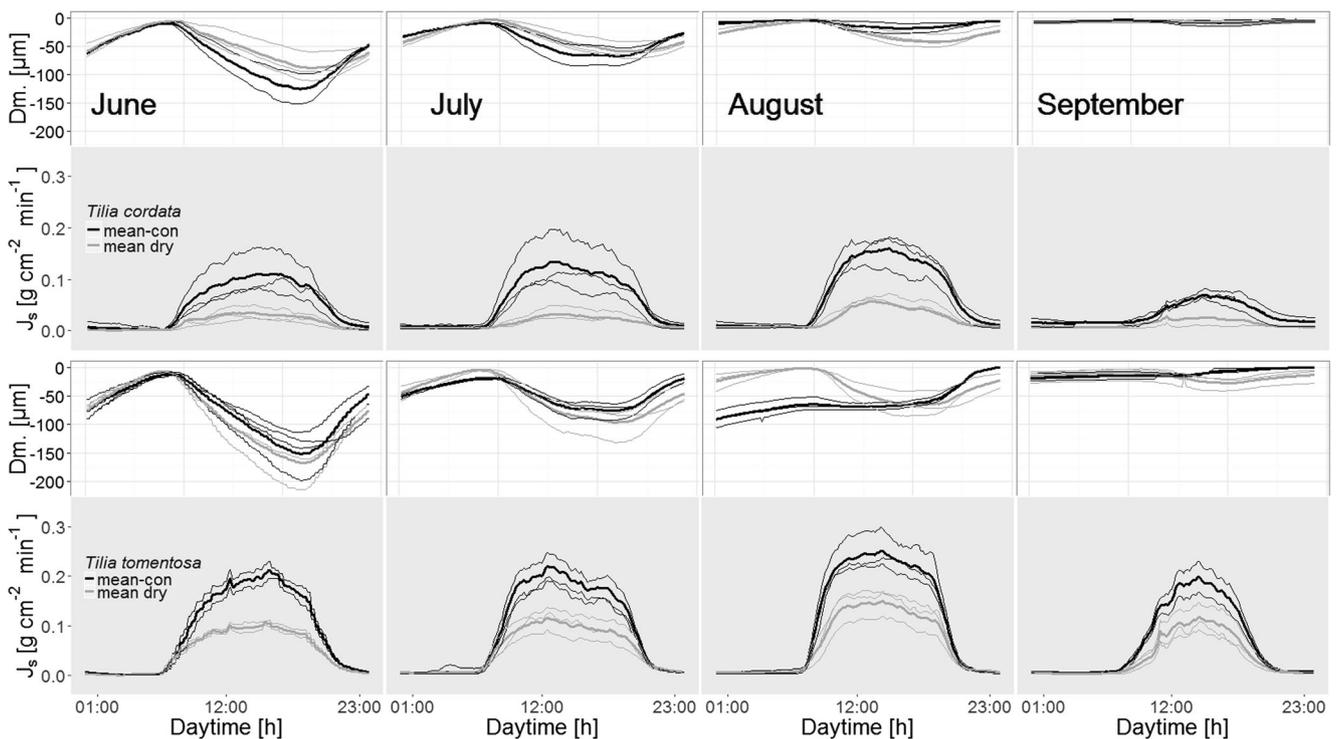


Fig. 3 Diurnal patterns of diameter change (Dm.) and sap flux density (J_s) for both *Tilia* species in the summer months in 2017. The data are the means of up to four replicates per species and treatment (thick curves) as well as of single trees (thin curves)

In the initial state (May—pre-drought), there were no con- and heterospecific differences in total fine root biomass (Fig. 4), but in the deepest measured soil layer (20–30 cm) both groups of *Tc* had significantly more fine roots than both groups of *Tt*. In September, however, *Tt*-con sharply increased in biomass at all measured soil depths by overall 161.2% to 259.78 g m⁻², whereas the fine root growth of *Tt*-dry was much less high (53.11%) and had a similar ($P = 0.572$) increment only in the 20–30 cm layer

compared to the control. In particular, in the upper-most soil layer (0–10 cm), there were severe biomass losses (May, 39.54; September, 7.29 g m⁻²).

Tc already showed relatively high amounts of fine root biomass in May but there was less strong subsequent increment at the deepest soil layer in comparison to *Tt*. *Tc*-dry was the only group where the root production was reduced by drought (18.1%) between the first and the second measurement campaigns due to dieback in the

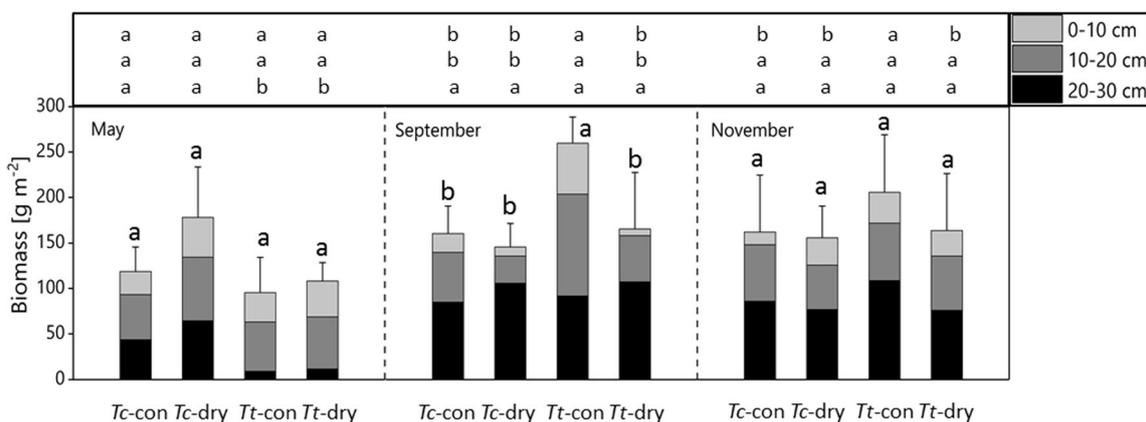


Fig. 4 Fine root development for both *Tilia* species under dry treatment and control conditions in May (pre-drought), September and November 2017. Data are means of four soil cores for each individual tree for the 0–10-cm, 10–20-cm and 20–30-cm layers, two of which were located at a

distance of 15 cm and the other two were located at a distance of 30 cm from the trunk. The different letters indicate significant differences ($p < 0.05$) between species and treatments for the overall fine root biomass (main plot) and the different soil layers (upper plot area)

upper parts of the soil (0–20 cm); therefore, it had the lowest overall fine root biomass of all four groups.

Sap flux response to environmental conditions

In most of the control cases, exponential saturation models best described the relationships between daily J_S with PAR. For *Tc*, however, we found linear correlations for June and September. When analysing the J_S for the entire year in different PAR and D_Z value ranges, we saw that *Tc* exhibited the smallest increase in its J_S at low PAR and D_Z , whereas *Ap* and *Tt* had their largest increases in these cases, as is highlighted by the values of the parameter b in the models (data not shown). At

medium PAR and D_Z , *Ap* and *Tc* had the highest increases and the LR-species *Ac* and *Oc* showed the strongest reductions in their J_S . Finally, very high PAR and VPD caused the highest slopes in *Tc*, whereas *Ap* had the largest reductions.

Further, the daily sums of the J_S of the control treatment had in each case a high negative correlation with the mean VWC, which means that they exhibited their highest J_S when the soil moisture was low. For the dry treatments, the J_S of both *Acer* species were negatively affected by high VWC (r_S *Ap*, -0.68 ; r_S *Ac*, -0.32 , $P < 0.001$), whereas *Tc* was the only species whose water use significantly decreased with decreasing VWC for the full year (r_S 0.35 , $P < 0.01$). *Tt* showed no clear tendency (r_S 0.01 , not significant).

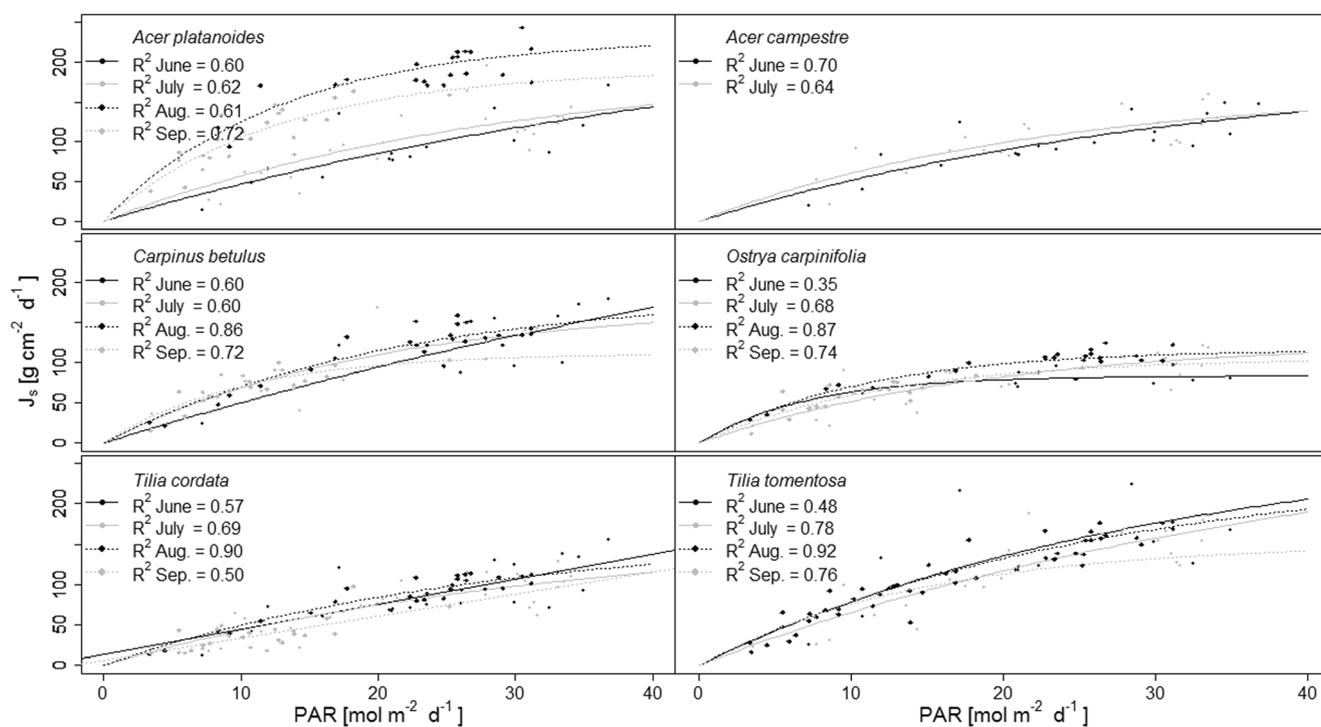


Fig. 5 Daily sums of the sap flux density (J_S) versus the daily cumulative photosynthetically active radiation (PAR) for the six species in the control treatment for the summer months of 2017. Each panel represents the mean of all trees measured per species. Lines through the data are

exponential saturation curves in the form of $y = a(1 - \exp(-bx))$ or linear models, and the coefficients of determination (R^2) are given for each month. Due to the lack of data for *Acer campestre* in August and September, there could no models be calculated for these months

Discussion

Effects of drought on phenology, growth and water use

Generally, we saw an earlier leafing and senescence for the native species (including *Ac*) compared to the non-native species *Oc* and *Tt*, which had on average longer vegetation periods. Same as it is known for populations originating from different localities within a species range (Lechowicz 1984), it can also be assumed that species from warmer regions have higher requirements for cumulative thermal sums prior to leafing. Therefore, it is understandable that *Ac*, which is a native species but originates from a relatively dry habitat, appeared as an intermediate-leafing species. The late spring phenological development may have helped *Oc* and *Tt* to be less affected by the early summer dryness, because transpiration and, therefore, soil water exploitation started relatively late.

On average, LR species in the dry treatment exhibited greater losses in growth compared to HR species as well as stronger diurnal stem shrinkage (measured only for *Tilia*) during the hottest hours of the day. Daily variations in the stem diameters occur because the negative water balance in the leaves in times of high evaporative demand is temporarily compensated by the relocation of water from water-rich stem tissues (Larcher 2001). Using stem water reserves at a higher rate may have helped *Tt* to retain its transpiration at a relatively high constant level compared to *Tc*.

The high resistance in terms of growth and J_S that we saw for both *Acer* species was also found by Kunz et al. (2016). In their drying experiment with potted seedlings, *Ap* under dry treatment did not show a significant decrease in its maximum photosynthetic rate. They also measured high water use and stomatal conductance of *Ap* and *Ac*, with transpiration and stomatal conductance of *Ap* being slightly less affected than those of *Ac*, and none of the plants within the *Acer* genus died from drought, in contrast to the other four investigated species.

Carbon allocation

The interspecific differences in root accessibility to soil water and the amount of absorbing root surface can account for differences in water use and drought tolerance. With increasing dryness, root-shoot-ratios or fine root biomass may decrease in some places in the soil, while elsewhere roots can continue extending and branching. This is a phenomenon frequently observed in plants with deep root systems growing in dry areas. Larcher (2001) also mentioned that plants are able to actively lower their root potentials to exploit more soil water, with xerophytes achieving the highest tensions of less than -6 MPa.

For *Tilia*, we observed that soil drying negatively affected the fine root biomass in the upper parts of the soil but stimulated growth into deeper parts likely to tap into additional water reserves. Comparing above- and belowground data suggests, that for *Tt*, the drying procedure led to an investment of carbon into fine root development at the cost of aboveground growth or stagnation. Due to the limited measurement depth (0–30 cm), we cannot rule out the possibility that fine roots developed at even lower soil depths or grew outside the 30 cm radius. This budgeting could be one reason why *Tt* could maintain higher sap flux than *Tc*, which is known by the practitioners to invest more in twig growth until autumn. Therefore, the maintenance of high stem growth alone seems not to be no a suitable indicator for drought tolerance.

In the study of Kunz et al. (2016), *Ap* und *Ac* were the only species where the root-shoot-ratios did not decline significantly due to the drought treatment. Under water shortage, *Ac* exhibited the highest and *Ap* the second highest ratio by far compared to the other investigated species. If applicable to our individuals, this could explain why *Ac*-dry showed a relatively high resistance in J_S . Due to the even higher VWC values in the dry treatment plot of *Ap* compared to the control plot, it is unknown why this group did not reach an even higher J_S . We assume that the frequent inundation at this plot caused fine root growth inhibition, which is the main reason for insufficient water supply at such sites (Larcher 2001).

Tolerance to water potential and stomatal diffusion resistances

Larcher (2001) mentioned that the response threshold and the effectiveness of the stomatal aperture, as well as the minimum water potentials at which trees reach their activity limits, are plant or species specific and decisive for their distribution. It is also known that different leaf anatomical characteristics influence the water-use behaviour (Roloff et al. 2013). Klein (2014) found species from Mediterranean forests and semi-arid woodlands maintaining water use at significantly lower leaf water potentials than trees from tropical and temperate forests, and Roloff et al. (2013) mentioned that, in most cases tree species from dry habitats are better at lowering their water potentials to exploit additional water reserves. Choat et al. (2012) found a tight link between the embolism resistance and the level of drought stress experienced by plants in their native environments. These results can be used to explain why our LR species showed a good overall performance under drought. It is likely that *Tc* in turn was reaching its lower critical limit of soil water potential, because it was the only species in the dry treatment where the J_S was negatively correlated to the soil moisture.

Köhler (2010) used hyperbolic response functions to account for the influence of radiation on the J_S and Oren et al. (1999) and Gillner et al. (2017) mentioned that the stomata close

progressively as atmospheric drought progresses (here VPD), so that transpiration increases to a plateau and sometimes subsequently decreases again as VPD is maximised. Accordingly, we found in most cases the behaviour of daily water use relative to the atmospheric drivers PAR and VPD (Oren et al. 1999; Peters et al. 2010) is described best using non-linear response functions (exponential saturation curves; Fig. 5).

Ap and the LR species showed more conservative water use when there was a high evaporative demand than did *Tc* and *Cb*, whose curves did not show equal flattening at high VPD and PAR. This was likely due to stomata regulating leaf water status (Oren et al. 1999; Peters et al. 2010). At low radiation levels, however, the water use of the LR species and *Ap* showed higher slopes. Oren et al. (1999) mentioned that species that exhibit high stomatal conductance at low VPD need a higher sensitivity at high VPD, as required by the role of stomata in regulating transpiration and water potential.

The main reason for the very low J_S of *Tc*-dry remains unclear. We assume that it was due to an insufficient water uptake capacity and because the early phenological and fine root development have led to a rapid exploitation of the soil water resources, which encountered very dry conditions in the early summer. We doubt however the possible explanation of consistently high stomatal control because other studies have shown that *Tc* is following a tolerance strategy indicated by decreasing values of minimum leaf water potential at increasing drought (Fini et al. 2009; Gillner et al. 2017). Additionally, Choat et al. (2012, Supplementary Material) showed a notable higher embolism resistance of *Tc* and *Cb* in comparison to both *Acer* species, which had quite similar values. If the embolism formation sets the threshold for stomatal closure (Choat et al. 2012), *Cb* and *Tc* should exhibit less stomatal control, as we have assumed for the control treatment.

Maintaining open stomata under drought leads to a high risk of damage or death via cavitation and possibly to a breakdown in physiological performance, as well as early onset of leaf wilting and abscission. Even if leaf shedding could be a way to avoid xylem cavitation (Choat et al. 2012; Roloff et al. 2013; Kunz et al. 2016), if premature leaf-fall occurs too frequently, trees will likely not be able to accumulate a sufficient amount of reserve substances.

Conclusions—putting the right tree in the right place

Considering the expectation for a higher frequency of drought events and more arid climates due to climate change, some plant species will lose their climatic suitability, in particular for plantings in harsh urban environments. Drought- and heat-induced tree die-offs have recently been observed and are likely to continue to increase (Choat et al. 2012).

Trees in cities are known to provide microclimatic thermal regulation via evapotranspiration and shading (Shashua-Bar and Hoffmann 2000; Armson 2012; Gillner et al. 2015). The

latter plays a major role in determining the cooling effect (Shashua-Bar and Hoffmann 2000), which suggests that species that show early leaf senescence and abscission due to drought will provide distinctly reduced and shortened thermal benefits. Under strong dryness conditions, our results suggest higher plant cooling to be provided by LR species, which could maintain relatively high transpiration rates and did not show signs of senescence or leaf-fall during the summer and early autumn. This was due to a longer growing season and because they exhibited more active precautions against drought, which enabled them to maintain important physiological processes.

With our results, we hope to improve the right choice of species for the respective planting situations. Encouraged by the findings of other researchers, we estimate a high drought tolerance for *Ac* and therefore recommend planting this species at drought-prone sites. Within the *Tilia* genus, we believe that *Tt* is more appropriate for these sites, whereas *Tc* should be rather planted in park-like environments with a sufficient water supply. This also applies to *Cb*, although it showed a better performance than *Tc*. *Oc* in turn showed the most typical behaviour that is commonly assumed for species from dry habitats and its good performance is in line with the species ranking of Niinemets and Valladares (2006). This species can be very useful for roadsides and other harsh planting sites. Because of the spatial bias for *Ap*-dry caused by the exceptionally high soil moisture contents (Fig. 1), we cannot make any reliable predictions about the drought tolerance of this species. This shows an obvious limitation of our experimental setting and leads us to conclude that for future studies, a completely randomised design with individual trees as independent replicates or similar should be preferred.

As in most studies, our species number was limited to only a few because doing such comparative studies is difficult and resource demanding. We surely need to conduct additional research to understand the differences in the species responses to environmental conditions and, in particular, drought events. But more importantly is to systematise and bundle results obtained in experimental studies to develop sound classifications and typologies of trees that go beyond the species level. Useful categories could be the wood anatomy (Klein 2014), the plant functional type (Peters et al. 2010) or, as we have studied, the native habitat (Klein 2014; Sjöman et al. 2012; Stratopoulos et al. 2018). On this basis, more systematic screening of species from dry habitats should be undertaken to broaden the species choice. Rigorous experimental testing should provide the evidence base for targeted selection and planting of trees in cities. Such knowledge can help architects and urban planners make informed decisions and to achieve a better capability of the planted trees for providing ecosystem services.

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Compliance with ethical standards The experiments comply with the current laws of Germany.

Conflict of interest The authors declare that they have no conflict of interest.

References

- Armson D (2012) The effect of trees and grass on the thermal and hydrological performance of an urban area dissertation, University of Manchester
- Armson D, Stringer P, Ennos AR (2012) The effect of tree shade and grass on surface and globe temperatures in an urban area. *Urban For Urban Green* 11:245–255. <https://doi.org/10.1016/j.ufug.2012.05.002>
- BBCH (2001) Entwicklungsstadien mono- und dikotyler Pflanzen. BBCH Monografie. <https://doi.org/10.5073/bbch0514>
- Chapin FS III, Autumn K, Pugnaire F (1993) Evolution of suites and traits in response to environmental stress. *Am Nat* 142:78–92. <https://doi.org/10.1086/285524>
- Choat B, Jansen S, Brodribb TJ, Cochard H, Delzon S, Bhaskar R, Bucci SJ, Field TS, Gleason SM, Hacke UG, Jacobsen AL, Lens F, Maherali H, Martínez-Vilalta J, Mayr S, Mencuccini M, Mitchell PJ, Nardini A, Pittermann J, Pratt RB, Sperry JS, Westoby M, Wright IJ, Zanne AE (2012) Global convergence in the vulnerability of forests to drought. *Nature* 491:752–755. <https://doi.org/10.1038/nature11688>
- Duhme F, Pauleit S (2000) The dendrofloristic richness of SE-Europe, a phenomenal treasure for urban plantings. *Mitteilungen aus der Biologischen Bundesanstalt für Land- und Forstwirtschaft Berlin-Dahlem* 370:23–29
- DWD (2018) www.dwd.de. Accessed 15 March 2018
- Endlicher W, Jendritzky G, Fischer J, Redlich JP (2008) Heat waves, urban climate and human health. In: Marzluff JM et al (eds) *Urban ecology*. Springer, Boston, pp 269–278
- Esri (2014) ArcGIS
- Ewers BE, Oren R, Johnsen KH, Landsberg JJ (2001) Estimating maximum mean canopy stomatal conductance for use in models. *Can J For Res* 31:198–207. <https://doi.org/10.1139/x00-159>
- Fini A, Ferrini F, Frangi P, Amoroso G, Piatti R (2009) Withholding irrigation during the establishment phase affected growth and physiology of Norway maple (*Acer platanoides*) and linden (*Tilia* spp.). *Arboricult Urban For* 35:241–251
- GALK (2018) GALK-Straßenbaumtest 1 and 2. www.galk.de. Accessed 01 March 2018
- Gill SE, Handley JF, Ennos AR, Pauleit S (2007) Adapting cities for climate change: the role of the green infrastructure. *Built Environ* 33:115–133
- Gillner S, Vogt J, Tharang A, Dettmann S, Roloff A (2015) Role of street trees in mitigating effects of heat and drought at highly sealed urban sites. *Landsc Urban Plan* 143:33–42. <https://doi.org/10.1016/j.landurbplan.2015.06.005>
- Gillner S, Korn S, Hofmann M, Roloff A (2017) Contrasting strategies for tree species to cope with heat and dry conditions at urban sites. *Urban Ecosyst* 20:853–865. <https://doi.org/10.1007/s11252-016-0636-z>
- Granier A (1987) Evaluation of transpiration in a douglas-fir stand by means of sap flow measurements. *Tree Physiol* 3:309–319
- Hiemstra JA (2011) Straßenbaumtest in den Niederlanden. *Veitshöchheimer Berichte* 152:37–41
- Kiermeier P (1995) Die Lebensbereiche der Gehölze eingeteilt nach dem Kennziffernsystem. Pinneberg
- Klein T (2014) The variability of stomatal sensitivity to leaf water potential across tree species indicates a continuum between isohydric and anisohydric behaviours. *Funct Ecol* 28:1313–1320. <https://doi.org/10.1111/1365-2435.12289>
- Köhler M (2010) Cacao agroforestry under ambient and reduced throughfall – tree water use characteristics and stand water budgeting. Dissertation, University of Göttingen
- Kunz J, Räder A, Bauhus J (2016) Effects of drought and rewetting on growth and gas exchange of minor European broadleaved tree species. *Forests* 7:239. <https://doi.org/10.3390/f7100239>
- Larcher W (2001) *Ökophysiologie der Pflanzen*. Ulmer Verlag, Stuttgart
- Lechowicz MJ (1984) Why do temperate deciduous trees leaf out at different times? Adaptation and ecology of forest communities. *Am Nat* 124:821–842. <https://doi.org/10.1086/284319>
- LWG (2018) Forschungsprojekt Stadtgrün 2021. Neue Bäume braucht das Land. www.lwg.bayern.de. Accessed 26 April 2018
- McCarthy HR, Pataki DE, Jenerette GD (2011) Plant water-use efficiency as a metric of urban ecosystem services. *Ecol Appl* 21:3115–3127. <https://doi.org/10.1890/11-0048.1>
- Moser A, Rahman MA, Pretzsch H, Pauleit S, Rötzer T (2017) Inter- and intraannual growth patterns of urban small-leaved lime (*Tilia cordata* mill.) at two public squares with contrasting microclimatic conditions. *Int J Biometeorol* 61:1095–1107. <https://doi.org/10.1007/s00484-016-1290-0>
- Niinemets Ü, Valladares F (2006) Tolerance to shade, drought, and water logging of temperate northern hemisphere trees and shrubs. *Ecol Monogr* 76:521–547. [https://doi.org/10.1890/0012-9615\(2006\)076\[0521:TTSDAW\]2.0.CO;2](https://doi.org/10.1890/0012-9615(2006)076[0521:TTSDAW]2.0.CO;2)
- Oren R, Sperry JS, Katul GG, Pataki DE, Ewers BE, Phillips N, Schäfer KVR (1999) Survey and synthesis of intra- and interspecific variation in stomatal sensitivity to vapour pressure deficit. *Plant Cell Environ* 22:1515–1526. <https://doi.org/10.1046/j.1365-3040.1999.00513.x>
- Peters EB, McFadden JP, Montgomery RA (2010) Biological and environmental controls on tree transpiration in a suburban landscape. *J Geophys Res* 115:G04006. <https://doi.org/10.1029/2009JG001266>
- R Core Team (2014) R: A language and environment for statistical computing
- Rahman MA, Moser A, Rötzer T, Pauleit S (2017a) Microclimatic differences and their influence on transpirational cooling of *Tilia cordata* in two contrasting street canyons in Munich, Germany. *Agric For Meteorol* 232:443–456. <https://doi.org/10.1016/j.agrformet.2016.10.006>
- Rahman MA, Moser A, Rötzer T, Pauleit S (2017b) Within canopy temperature differences and cooling ability of *Tilia cordata* trees grown in urban conditions. *Build Environ* 114:118–128. <https://doi.org/10.1016/j.buildenv.2016.12.013>
- Roloff A (2013) Stadt- und Straßenbäume der Zukunft – Welche Arten sind geeignet? Aktuelle Fragen der Stadtbauplanung, -pflege und -verwendung, *Forstwissenschaftliche Beiträge Tharandt Beiheft* 14: 173–187
- Roloff A, Bärtels A (2006) *Flora Der Gehölze – Bestimmung, Eigenschaften Verwendung*. Ulmer Verlag, Stuttgart
- Roloff A, Grundmann B, Korn S (2013) Trockenstress-Toleranz bei Stadtbäumen – Anpassungs- und Schutzstrategien/Arteneignung. In: Dujesiefken D (ed) *Jahrbuch der Baumpflege*, 2013. Haymarket Media, Braunschweig, pp 173–185
- Shashua-Bar L, Hoffmann ME (2000) Vegetation as a climatic component in the design of an urban street: an empirical model for predicting the cooling effect of urban green areas with trees. *Energy Build* 31:221–235. [https://doi.org/10.1016/S0378-7788\(99\)00018-3](https://doi.org/10.1016/S0378-7788(99)00018-3)

Sjöman H, Gunnarsson A, Pauleit S, von Bothmer R (2012) Selection approach of urban trees for inner-city environments: learning from nature. *Arboricult Urban For* 38:194–204

Stratopoulos LMF, Duthweiler S, Häberle K-H, Pauleit S (2018) Effect of native habitat on the cooling ability of six nursery-grown tree species and cultivars for future roadside plantings. *Urban For Urban Green* 30:37–45. <https://doi.org/10.1016/j.ufug.2018.01.011>