Effects of Drought on the Phenology, Growth, and Morphological Development of Three Urban Tree Species and Cultivars

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Abstract: Under changing climatic conditions, drought may become a critical constraint for trees in urban areas, particularly at roadsides and highly paved squares. As healthy urban trees have proven to be an important mitigation and adaptation tool for climate change as well as a significant provider of ecosystem services, there is a need for planting species and cultivars capable of coping with the limited water supply. However, data on species' and cultivars' response to drought, particularly their water supplying root systems remains rare. To consider the whole plant responses to drought situations, we studied the growth and phenology of three frequently planted tree species and cultivars with a diameter of 5–6 cm during a one-year rainfall exclusion experiment conducted in a nursery field as well as the dry biomass of the compartments branch, stem, and root after excavation. Our results revealed that species' and cultivars' performance were linked to their within-plant carbon partitioning. A high tolerance to drought was noted for *Acer campestre*, with a particularly high ratio of root:shoot ratio, which made it presumably less susceptible to droughts. *Tilia cordata* 'Greenspire' was highly affected by the reduced water availability visible through prematurely leaf senescence, while *Carpinus betulus* 'Fastigiata' suffered from losing a considerable part of its root biomass, which resulted in the lowest root:shoot ratio of all species and cultivars. This study demonstrated the need for investigating the reaction patterns of species and cultivars by considering both the above-and the below-ground plant parts. We recommend that, for future tree plantings at harsh and challenging urban sites, an important selection criterion should be species' and cultivars' capability to develop and retain strong and dense root systems even under limited water supply, as that is believed to be an important trait for drought tolerance.

Keywords: allocation; drought tolerance; partitioning; resistance; root:shoot ratio

1. Introduction

During the course of climate change, higher temperatures along with shifts in the precipitation rate are estimated to increase drought severity and frequency [1]. This is also applicable for Central Europe [2] and may severely affect trees planted in paved urban environments in this region. Combined with the urban heat island effect caused by the properties of built structures, the absence of vegetation, and the anthropogenic heat emissions [3–5], the growth conditions of urban trees are even more challenging to those in natural environments [6–8]. As healthy urban trees have proven to be an important mitigation and adaptation tool for climate change as well as a huge provider of ecosystem services [9–12], there is a need for planting species and cultivars capable of coping with extreme climatic events such as prolonged droughts.

It is known that, to some extent drought-survival traits are genetically inherited [13] and those plants cope with drought conditions through structural, functional, and physiological adjustments. Research on selected urban tree species and cultivars revealed higher stomatal sensitivity under drought of trees from relatively dry habitats in comparison to trees from more mesic habitats [14]. It is also known that trees avoid extremely negative water potentials through a combination of internal water storage [15], reduced leaf area, and access to a larger volume of soil via the development of extensive root systems [16]. A recent field study on two linden cultivars [17] showed that trees with compact root systems around the stem tend to develop more fine roots laterally to increase their soil-to-root interface. In the long term, elevated root:shoot ratios can be regarded as an adaptation to dry sites [18] to make trees less susceptible to water shortage [19]. In the short term, however, moderate water stress can shift carbon allocation from growth to storage and resin defense [13], unless drought is severe enough to cause cessation of carbon allocation to all sinks.

Information about species' and cultivars' responses to stress is mainly derived from knowledge about the environmental conditions in their respective natural habitats [20,21]. Only some experimental urban and forest studies have compared the performance of different tree species and cultivars explicitly under dry growing conditions [19,22–24] and in the available urban studies, with the focus solely being on the above-ground processes. In the urban context, knowledge of below-ground biomass and its distribution as well as the changing patterns of carbon allocation to different tree compartments remains limited. In addition, research on the whole plant responses of urban trees needs to consider species- and cultivar-specific seasonal metabolic adaptations because of the superordinate impact on the timing of the physiological processes of trees.

Therefore, we studied the whole plant body when investigating the drought tolerance of different species and cultivars. We provided data on leaf development and the stem growth of trees with a diameter at 1 m height of 5–6 cm during a soil drying experiment of a complete growing cycle as well as values for biomass for the three compartments branches, stem, and roots after excavation of the trees from the field. The specific questions addressed by this study were based on the effect of drought on (1) the phenology, (2) growth, (3) biomass of branches, stems, and roots of three frequently planted native tree species and cultivars, as well as (4) species- and cultivar-specific within-plant carbon partitioning and allocation patterns, respective growth habits and the root system architectures, which may indicate the capacity of tree species and cultivars to respond to drought stress.

2. Materials and Methods

2.1. Study Site, Species and Cultivars Selection, and Drought Experiment

The study site municipal nursery (48°08′05″ N, 11°28′47″ E, 534 m a.s.l.) is located to the southwest of Munich, Germany. The long-term (1981–2010) annual means of the temperature and rainfall from the nearest weather station in the city center of Munich are 9.7 °C and 944 mm, respectively [25]. The 42 ha large area is characterized by an almost uniform topography and possible small microclimatic variations. The predominant soil types range from moderate sandy loam to strong loamy sand, as estimated by a finger test. Interpretation of the water-retention curves provided in the literature

indicated a soil moisture tension (pF value) of 1.8 (field capacity) between 29 Vol.-% and 33 Vol.-% volumetric soil water content (VWC) and a pF value of 4.2 (permanent witling point; PWP) at 12 Vol.-% and 16 Vol.-% for the moderate sandy loam and the strong loamy sand, respectively [26]. This PWP does not represent the true physiological wilting point for our investigated trees; however, it may instead be regarded as an indicator of severe drought stress [19]. This is because we did not determine PWP for each species and cultivar separately, rather obtained it from literature where it is set for agricultural plants only.

Six to eight trees each of the following temperate deciduous species and cultivars with a diffuse-porous wood anatomy and a diameter of 5–6 cm at 1 m height were selected: *Acer campestre* L. subsp. *campestre* (*Ac*), *Carpinus betulus* L. 'Fastigiata' (*Cb*), and *Tilia cordata* Mill. 'Greenspire' (*Tc*), which are frequently planted native species or cultivars. The study species and cultivars were assumed to vary in terms of drought and shade tolerance [27] (Table 1). The abbreviations of all the species and cultivars are listed in Table 1 and will be used hereinafter.

Table 1. The characteristics of the surveyed trees. Diameter at 1 m height is given for the experimental period May 2017.

	Code	Control *n*	Dry	Diameter [cm ± sd]		Shade Tolerance [1]	Drought Tolerance [1]
				Control	Dry		
Acer campestre	*Ac*	3	3	5.60 ± 0.25	5.66 ± 0.09	3.18 ± 0.14	2.93 ± 0.32
Carpinus betulus 'Fastigiata'	*Cb*	4	3	5.30 ± 0.14	5.61 ± 0.08	3.97 ± 0.12	2.66 ± 0.16
Tilia cordata 'Greenspire'	*Tc*	4	4	5.90 ± 0.10	6.00 ± 0.16	4.18 ± 0.16	2.75 ± 0.15

[1] Extracted from the meta analysis of (Appendix A in [27]), including data of 806 North American, European/West Asian, and East Asian temperate shrubs and trees. Tolerance scales range from zero (no tolerance) to five (maximal tolerance).

We employed an experimental setting where we simulated the conditions of a sustained drought to investigate the physiological and growth responses of the trees [15,28] as well as their phenological timings, the architecture of the root systems, and the carbon partitioning and allocation. The rainfall exclusion experiment started in May 2017 and was conducted throughout the growing period of the year until November. We installed waterproof, translucent tarpaulins (2 m x 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 at 3 m distance from the trees (Figure 1). The tent-like constructions prevented rain infiltration close to the tree stems. A second group was exposed to the prevailing weather conditions and served as a control ("con"). Each plot was made up of three to four plants per species/cultivar and treatment, which were all transplanted in the spring of 2014 in parallel rows at 2×3 m spacing. At the beginning of the drought stress study, no significant differences were noticed between the stem diameters of control in comparison to the dry treatment groups (Table 1).

2.2. Climate and Soil Moisture

A full suite of climatic variables was sampled every 10 min with a weather station (Davis Vantage Pro2; Davis Instruments, Hayward, USA) placed in an unshaded site approximately 200 m away from the experimental plots. Due to equipment failure, the 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.

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 away from the tree stems. For each species/cultivar and treatment, one sensor was used for one centrally located individual in the row. Ten-min means were calculated from 1 min readings and logged (CR800 connected to an AM16/32 B multiplexer, Campbell Scientific, Logan, UT, USA and Agilent 34970A Data Acquisition/Switch Unit, Agilent

Technologies, Santa Clara, CA, USA). Given that the continuous measurement devices failed several times probably due to the high soil compaction and drying, we additionally used a portable soil moisture mete (UMP-1, UGT, Müncheberg, Germany) for point measurements in the upper 10 cm of the soil layer during four days in the summer. The readings were made at defined distances from all study trees, as shown in Figure 2.
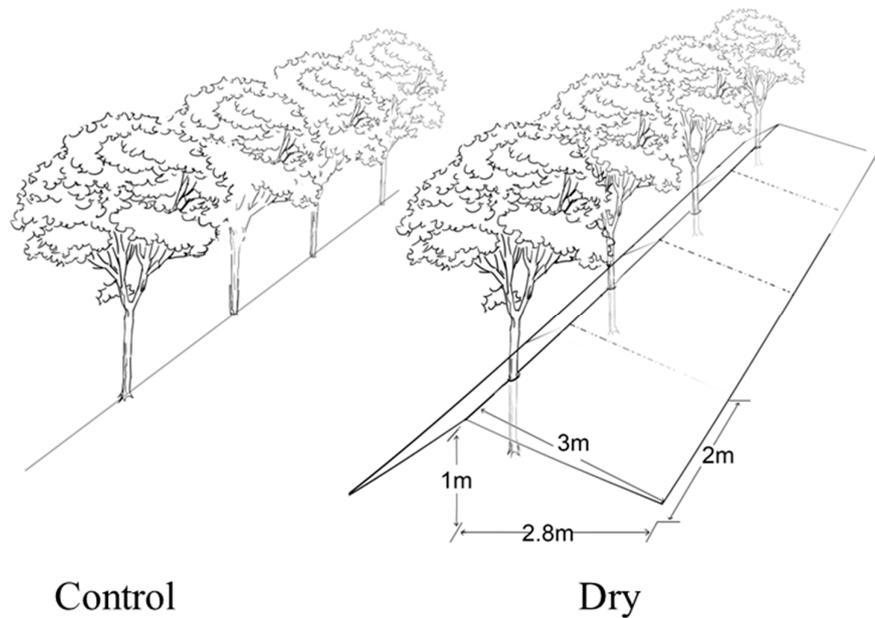

Figure 1. Schematic structure of the drought experiment. The rooting zones of the trees on the right were covered by the rainfall exclusion constructions ("dry"), whereas the trees on the left were exposed to the prevailing weather conditions.
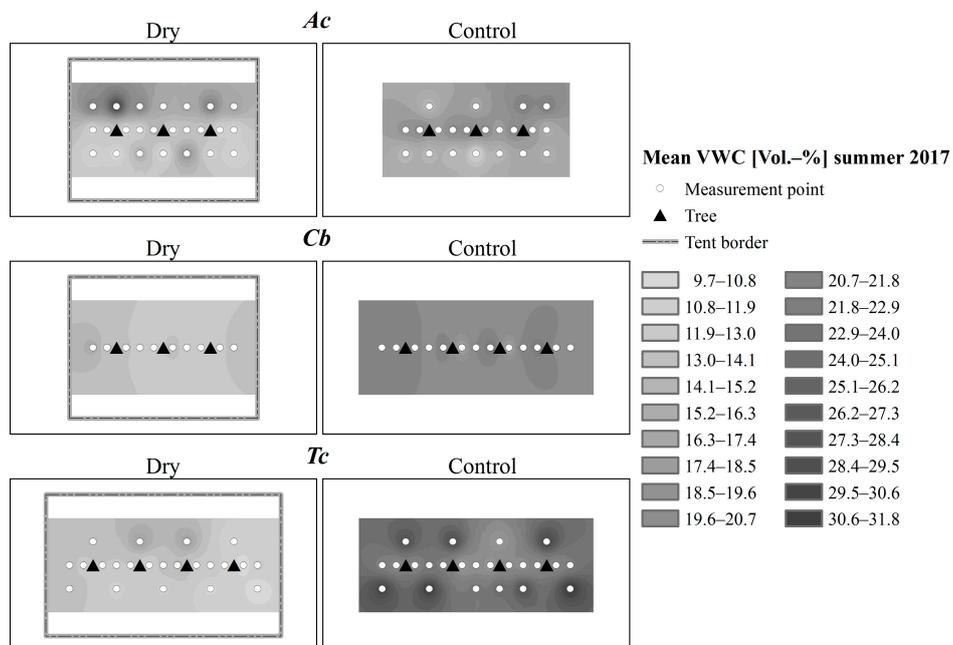

Figure 2. Maps (inverse-distance-weighted interpolation) of the volumetric soil water contents (Vol.-%; VWC) at a soil depth of 10 cm averaged over four measurement days in summer 2017 and collected at defined distances from the study trees. For full species and cultivar names see Table 1.

2.3. Spring and Autumn Phenology

We classified the spring and autumn phenology according to the BBCH (Biologische Bundesanstalt für Land- und Forstwirtschaft, Bundessortenamt und CHemische Industrie) phenological growth stages and identification keys [29]. All the phenological stages, from the beginning of bud swelling (BBCH 01) until the completion of leaf unfolding (BBCH 19) in spring and from the start of leaf discolouration (BBCH 91) until the end of leaf fall (BBCH 97) in autumn were coded once or twice a week between the end of March and the middle of May and between the beginning of October and the end of November, respectively. In addition, we made observations concerning early wilting symptoms throughout the entire study period.

2.4. Optical Measurements of Crown and Root System Architecture

The leaf area index (m^2 m^{-2}; LAI), which is the one-sided green leaf area per unit ground surface area, was determined using hemispherical photographs (Nikon Coolpix P5100 camera with fisheye lens and Mid-OMount, Nikon Corporation, Tokyo, Japan) analysed with the programme WinSCANOPY (Régent Instruments Inc., Quebec, Canada). Among the available several methods, we used the LAI-2000 generalised method based on the work of Miller [30] and Welles and Norman [31] for deriving the LAI. Data acquisition was performed under conditions with uniformly overcast sky in the middle of June, shortly after implementation of the drought experiment.

We also measured sufficient numbers of points (7–11 x, z pairs) to describe each of the trees' average crown shape. Geometric data were then processed within the software FV2200 (LI-COR Biosciences, Lincoln, USA) to compute the crown dimensions (volume and projected crown area) by using the model for isolated trees. Similarly, we also measured each trees' average root system dimensions after excavation in the winter 2017 (see the following section) and calculated the volumes with the FV2200 software.

Images of the top view of each root system were analysed by the open source image processing software ImageJ and the plugin DiameterJ [32], which is actually a nanofiber diameter characterization tool. First, the scenes were converted into black and white (i.e., binary) images, where the white pixels ideally represented the portions of the original image that were of interest (root system) and the black pixels represented the background. We compared the results of different segmentation algorithms (auto threshold) provided by the software and selected the appropriate algorithm, which best represented the root system. Inside each binary image, we then selected one rectangular area, where again segmentation most properly displayed the roots and eliminated the features of the image that we did not like to measure (e.g., scale bars or parts of the root system, where segmentation did not work well). This binary segment of the original image scene was used for analysis. The results included summary statistics such as mean root diameter and the percent of porosity.

2.5. Stem Growth Development, Excavation, and Dry Weight

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.

After leaf fall, all trees were excavated with a tree digger in November 2017 and cut into three compartments: Branches, stem, and roots. The root bales, cut at the root collar, were carefully washed to remove stones and soil and stored in the open air, similar to the other biomass. Fine roots (<2 mm) could not be preserved during this procedure. Subsequently, the biomass was oven dried at 65 °C for 72 h and then weighed using a balance with an accuracy of up to four decimal digits to obtain the dry weight, which is referred to hereafter as "biomass".

2.6. Statistical Analysis

We tested for significant differences for dry branch, stem, and root weight as well as the root:shoot ratio among the three species and cultivars. First, the datasets were tested for a normal distribution (Shapiro–Wilk test). Wherever necessary, data were log transformed in order to correct for skewness. To determine the effects of any treatment and species/cultivar, all data were subjected to two-way analysis of variance (ANOVA) for unbalanced designs with a significance level of α = 0.05. Further comparisons were made for the species/cultivar effect, since it contained more than two levels. To check for differences in the means of the species and cultivars we used one-way ANOVA for normally distributed data and the Kruskal-Wallis H as the non-parametric alternative and applied post-hoc tests (Tukey's post-hoc test and Dunn-Bonferroni test) for follow-up comparisons.

The resistance (R_{tc}) to drought was quantified as the ratio between the physiological performance during drought and normal conditions, as represented by the control plants [19], and the root:shoot ratio was calculated as the ratio between the root and above-ground dry mass. The above-ground biomass did not include the leaves of the trees and below-ground biomass not the fine roots (<2 mm), thereby the root:shoot ratio did not reflect investment of photosynthates between the whole above- and below-ground organs [18]. For all statistical analyses and their visualisation the software package R [33] was used. Measurements of VWC in 10 cm soil depth were processed and visualised with the help of ArcGIS, version 10.2.1 (Esri, Redlands, USA) [34]. 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.

3. Results

3.1. Environmental Conditions

After a strong return to cold weather in April, a midsummer-like temperature of 14.5 °C on average was measured in May. The month of June was also exceptionally warm, dry, and sunny with VPD values of > 30 (Figure 3) after strong precipitation events that occurred at the beginning of the month. As compared to the long-term (1981–2010) average, July and August with precipitation amounts of 137.9 mm and 139.3 mm, respectively were extremely rainy, alternating with high sunshine levels. In autumn, it was cold, rainy, and considerably cloudy for most of days. Snow fall and night frosts started in the middle of November [25].

The analysis of the soil moisture data confirmed a high correlation (r_S = 0.8) between the measurements at 10 and 30 cm, with the VWC being an average of 28.4% higher in the deeper soil layer. In 10-cm soil depth, the dry treatment plots showed significantly lower soil moisture contents (*P* = 0.004) in comparison to the control plots (Figure 2). Here, a minimum VWC value of 10.1 Vol.-% was measured for *Tc*-dry at the end of July (drop below the PWP). At 30 cm, the differences between the control and treatment groups for all the three species and cultivars were also significant (*P* < 0.001), which indicated the overall success of the rainfall exclusion experiment.

3.2. Leaf Phenology

Ac was less uniform concerning its timing of bud burst (BBCH 07) in comparison to *Cb* and *Tc* (Figure 3). For all the three tree species and cultivars, the completion of leaf expansion (BBCH 19) was observed during the second week of May. The fastest developing species/cultivar was *Tc*, where some individuals unfolded their leaves already at the beginning of May. In autumn, the timing of leaf fall among the different species/cultivars and treatments spanned several weeks. Individuals of *Tc*-dry were leafless (BBCH 97) in the middle of October but the onset of leaf discolouration (BBCH 92) was already observed in July (data not shown). In contrast, the drought conditions caused no difference in the timing of autumn phenology in *Cb* and *Ac*-dry kept its foliage even longer than *Ac*-con.
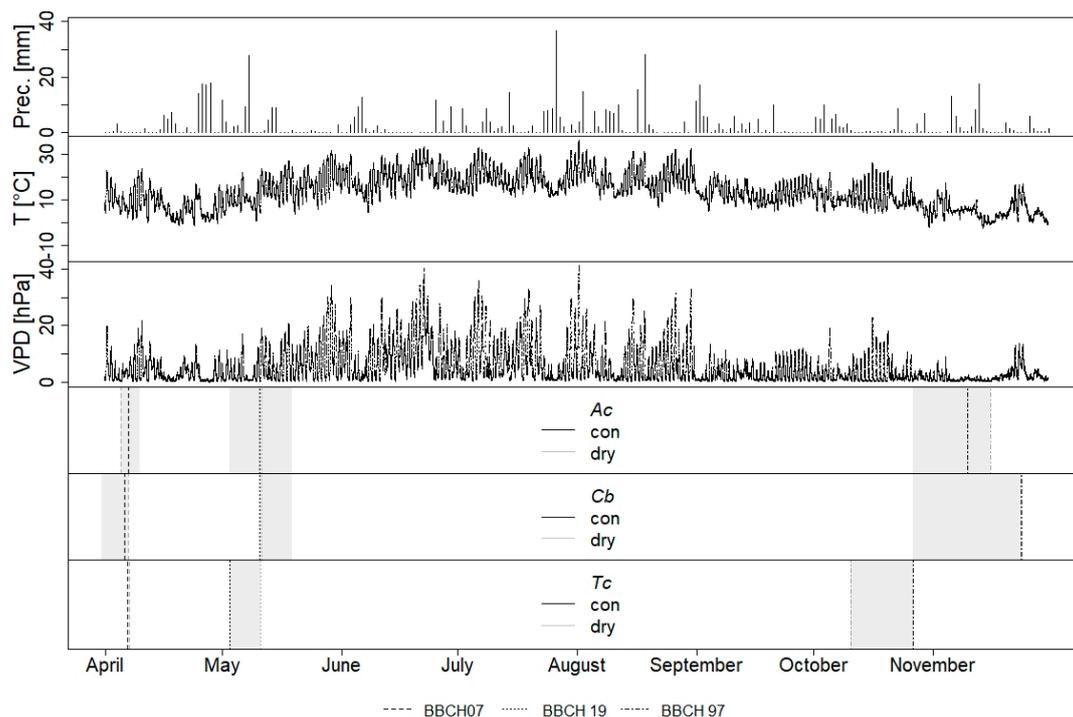
Figure 3. Daily amounts of precipitation (mm), temperature (°C), and vapour pressure deficit (hPa) was noted for the entire study period in 2017, as well as the phenological timing of the three species and cultivars under drought treatment (grey) and normal conditions (black). The vertical lines indicate the dates for the beginning of bud burst (BBCH 07), the completion of leaf folding in spring (BBCH 19), and the end of leaf-fall in autumn (BBCH 97), respectively, and represent the median of the observed trees per species/cultivar and treatment. The grey bars mark the time periods during which the phenological progresses occurred. Gaps in the meteorological data were replaced with the data from the German Weather Service (DWD; available online) measured in the Munich City Centre. For full species and cultivar names see Table 1.

3.3. Stem Growth

Stem diameter growth in the control plot and in relation to water shortage was analysed for the entire year of 2017 (Figure 4). For *Tc*, the growth in both the treatments had a distinct maximum value in May and almost stagnated toward autumn. Concerning the yearly diameter growth, this cultivar showed medium resistance to drought ($R_{tc} = 0.46$). *Ac* showed the maximum growth later in the year in the months of August and showed lowest biomass losses of all species and cultivars. *Cb*-con exhibited its highest growth in the months of June and July. The growth of *Cb*-dry was strongly impacted in June, which was exceptionally warm and dry (Figure 3). Its stem diameter decrease in this month was the highest from all species and cultivars, which was the main reason for its extremely low resistance value calculated for the entire whole year ($R_{tc} = 0.21$).

3.4. Biomass Partitioning and Allocation

Species/cultivar and treatment had always a significant effect on biomass, whereas the species/cultivar was the stronger influencing variable in each of the three cases (Table 2, Figure 5). Generally, the largest proportion of biomass was measured at the trunk section, followed by the root system. The branches had the lowest share.
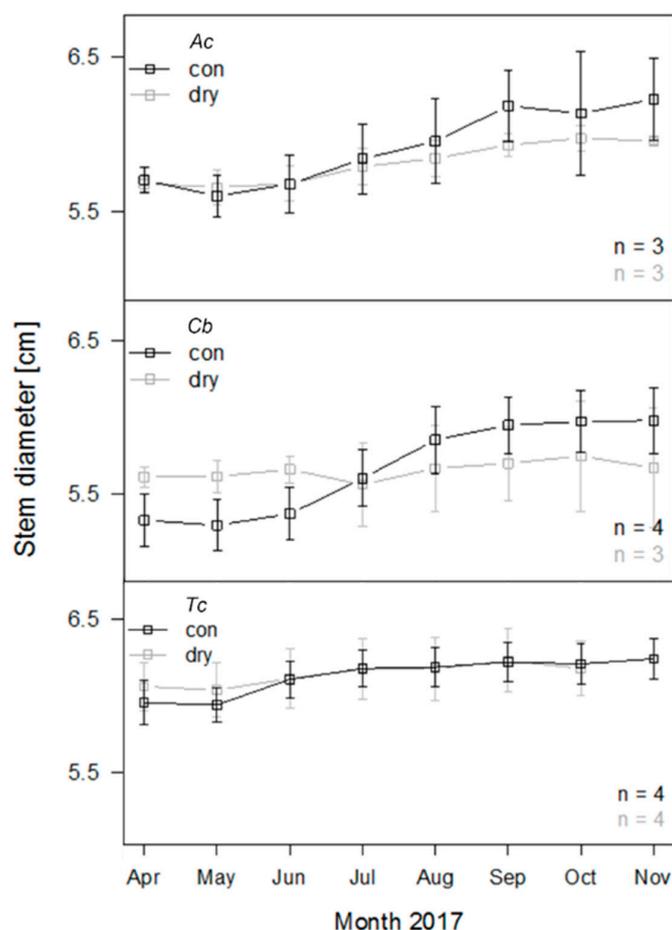
Figure 4. Stem diameter growth of all investigated species/cultivars and treatments (dry and control) for the entire study period in 2017 measured at a height of 1 m at the beginning of each month. The panel represents the mean of all trees per species/cultivar and the treatment and error bars indicate standard deviation. For full species and cultivar names see Table 1.

For the branch biomass, *Ac*-con reached highest (1121.33 ± 177.46 g), and *Cb*-dry and *Tc*-dry lower mean values (365.33 ± 60.34 and 308.50 ± 49.10 g), respectively. Species/cultivar and treatment strongly influenced ($p < 0.001$) the whole branch biomass of a tree.

For stem biomass, *Ac* showed the highest values in the control group (6162.33 ± 1204.59 g), and the lowest values were noted for *Tilia* in both the treatments (con: 4089.25 ± 220.16 g, dry: 3407.00 ± 322.40 g). *Ac* and *Cb* exhibited higher resistance (R_{tc} = 0.92 and 0.96, respectively) in comparison to *Tc* which lost more biomass due to the rainfall exclusion (R_{tc} = 0.83). The treatment effect was a bit smaller ($P = 0.0146$) in comparison to the dry branch and root weight.

For roots, *Ac*, both in the control and dry treatments, had more biomass than any other group (con: 5280.00 ± 467.73, dry: 3830.00 ± 186.62 g) despite the strong treatment effect. *Cb*-dry and *Tc*-dry showed the lowest values (1338.67 ± 89.39 and 1291.75 ± 25.66 g), as was also noted for the branch biomass.

For the root:shoot ratios, a very high ($P = 0.005$) treatment effect was observed. The roots of *Ac*-con and *Ac*-dry reached the highest values (0.73 ± 0.08 and 0.59 ± 0.02 g g^{-1}), and *Cb*-dry and *Tc*-dry showed the lowest average values (0.25 ± 0.01 and 0.35 ± 0.03 g g^{-1}), respectively.

Table 2. Weight (g) of dry branch, stem, and root biomass of the three study species and cultivars grown under the control and treatment conditions. Descriptive statistics and resistance with respect to the control (Rtc) are given as well as results from two-way ANOVA with treatment and species/cultivar as the fixed effects. P-values are given for a significance level of 0.05. n.s. indicates not significant, * statistically significant ($P < 0.05$), ** highly significant ($P < 0.01$), and *** very highly significant ($P < 0.001$). For full species and cultivar names see Table 1.

Dry Weight (g)	Group		n	Mean	±SD	Min	Media	Max	R_{tc}	Drought Effect Species/Cultivar Effect
Branch	Ac	con	3	1121.33	177.46	920	1189	1255	0.70	
		dry	3	785.00	89.50	696	784	875		
	Cb	con	4	593.25	8.54	588	590	606	0.61	$P < 0.001$ ***
		dry	3	365.33	60.34	309	358	429		$P < 0.001$ ***
	Tc	con	4	445.75	31.02	415	442	485	0.69	
		dry	4	308.50	49.10	243	317	358		
Stem	Ac	con	3	6162.33	1204.59	5015	6055	7417	0.92	
		dry	2	5652.50	127.99	5562	5652	5743		
	Cb	con	4	5226.75	315.97	4862	5276	5492	0.96	$P = 0.0544$ n.s.
		dry	3	5007.67	389.79	4592	5066	5365		$P < 0.001$ ***
	Tc	con	4	4089.25	220.16	3817	4102	4336	0.83	
		dry	4	3407.00	322.40	2962	3480	3707		
Roots	Ac	con	3	5280.00	467.73	4938	5089	5813	0.73	
		dry	3	3830.00	186.62	3628	3866	3996		
	Cb	con	4	2440.25	219.50	2193	2422	2725	0.55	$P < 0.001$ ***
		dry	3	1338.67	89.39	1271	1305	1440		$P < 0.001$ ***
	Tc	con	4	1869.00	63.59	1807	1863	1943	0.69	
		dry	4	1291.75	25.66	1266	1290	1321		
Root:Shoot Ratio	Ac	con	3	0.73	0.08	0.68	0.70	0.82	0.81	
		dry	3	0.59	0.02	0.58	0.59	0.60		
	Cb	con	4	0.42	0.02	0.40	0.41	0.45	0.60	$P = 0.005$ **
		dry	3	0.25	0.01	0.24	0.25	0.26		$P < 0.001$ ***
	Tc	con	4	0.41	0.03	0.39	0.40	0.45	0.85	
		dry	4	0.35	0.03	0.33	0.34	0.39		

3.5. Species/Cultivar-Specific Adaptation and Changes of Tree Shapes with Drought

Tc was the smallest species/cultivar concerning height (con: 5.13 ± 0.22 m, dry: 5.23 ± 0.18 m) (Table 3), but the narrow and pyramidal shaped *Cb* reached the lowest maximum canopy radius (con: 28.50 cm ± 1.50 cm, dry: 21.33 ± 0.94 cm) and canopy volume (con: 0.36 m ± 0.09 m^3, dry: 0.11 ± 0.55 m^3). LAI was lowest for *Ac* in both the treatments (con: 1.52 ± 0.11 m^2 m^{-2}, dry: 1.81 ± 0.14 m^2 m^{-2}). *Cb* reached highest values, especially in the dry treatment (con: 3.01 ± 0.87 m^2 m^{-2}, dry: 4.11 ± 1.49 m^2 m^{-2}). *Ac* and *Cb* showed the deepest rooting system in the control and dry treatments and exhibited a medium rooting width. The root system of *Cb*, however, was less dense in comparison to that of *Ac*, especially in the control treatment, where this cultivar showed the highest porosity of all species/cultivars (0.33 ± 0.05%). *Tc* exhibited medium rooting depth in both the treatments (con: 28.50 ± 1.50 cm, dry: 29.00 ± 1.41 cm), but the lowest rooting width of all species/cultivars (con: 30.75 ± 1.75 cm, dry: 28.67 ± 2.77 cm). For *Tc*, soil drying showed the biggest effect on the porosity of the root system (con: 0.24 ± 0.01, dry: 0.38 ± 0.04) and, therefore, the rooting density. No effect was noted for *Ac* (con: 0.30 ± 0.03, dry: 0.30 ± 0.05), while only a little effect was noted for *Cb* (con: 0.33 ± 0.05, dry: 0.34 ± 0.03).

Table 3. The above- and below-ground dimensions of the three investigated species and cultivars and the respective treatments (control and dry) as well as the density of foliage and root system are expressed by the means of leaf area index (m^2 m^{-2}; LAI) and the percent of porosity of the root system, respectively.

|	Above-Ground							
Code	Height [m ± sd]		Max. Canopy Radius [cm ± sd]		Canopy Volume [m^3 ± sd]		LAI [m^2 m^{-2} ± sd]	
	Control	Dry	Control	Dry	Control	Dry	Control	Dry
Ac	5.90 ± 0.14	6.00 ±0.00	48.33 ± 8.06	50.00 ± 9.63	0.64 ± 0.25	0.67 ± 0.23	1.52 ± 0.11	1.81 ± 0.41
Cb	5.90 ± 0.25	5.53 ±0.17	28.50 ± 1.50	21.33 ± 0.94	0.36 ± 0.09	0.11 ± 0.55	3.01 ± 0.87	4.11 ± 1.49
Tc	5.13 ± 0.22	5.23 ±0.18	43.00 ± 17.45	52.50 ±11.37	0.65 ± 0.20	0.68 ± 0.22	2.53 ± 0.25	2.13 ± 0.24
	Below-Ground							
Code	Rooting Depth [cm ± sd]		Max. Rooting Width [cm ± sd]		Root Volume [m^3 ± sd]		Porosity Root System [% ± sd]	
	Control	Dry	Control	Dry	Control	Dry	Control	Dry
Ac	30.33 ± 7.85	29.67 ± 0.47	31.00 ± 2.75	29.92 ± 2.00	0.050 ± 0.019	0.056 ± 0.008	0.30 ± 0.03	0.30 ± 0.05
Cb	30.00 ± 0.00	30.00 ± 0.00	32.25 ± 0.98	29.00 ± 2.01	0.057 ± 0.005	0.036 ± 0.007	0.33 ± 0.05	0.34 ± 0.03
Tc	28.50 ± 1.50	29.00 ± 1.41	30.75 ± 1.75	28.67 ± 2.77	0.058 ± 0.000	0.047 ± 0.009	0.24 ± 0.01	0.38 ± 0.04
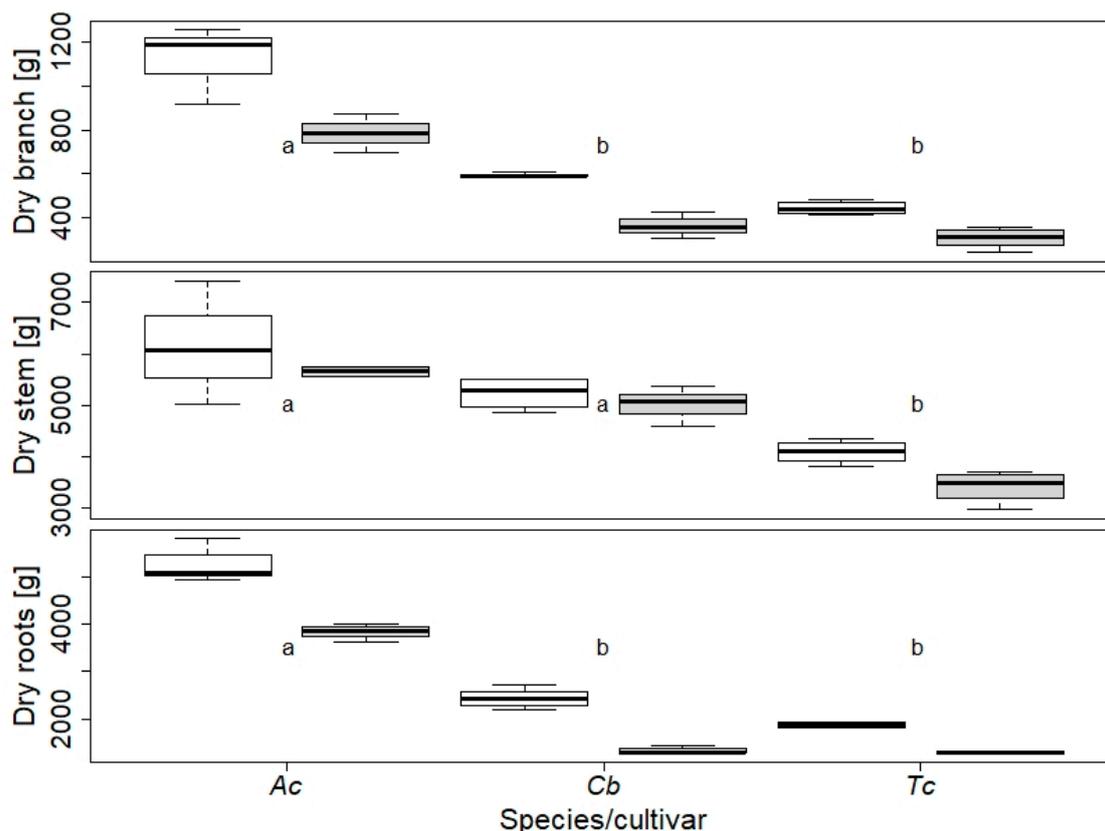
Figure 5. Box plots for dry branch, stem, and root weight (g) for the three study species and cultivars of the control (white box plots) and dry treatments (grey box plots). Small letters indicate the results of the follow-up comparisons for the species/cultivar effect; means are significantly different ($P < 0.05$) when indicated by different letters. For full species and cultivar names see Table 1.

4. Discussion

4.1. Drought Resistance and Within-Plant Carbon Partitioning and Allocation

In our study, we observed various degrees of above- and below-ground biomass gains and losses under drought, suggesting different strategies and abilities of tree species and cultivars to cope with this stressor. Generally, biomass as well as the root:shoot biomass dynamics and the root densities were significantly affected by the strong drought applied.

Among the species and cultivars, *Acer campestre* showed the most uniformly distributed losses over the entire plant body under drought, not as *Carpinus betulus* 'Fastigiata', for example, which showed more specific allocation patterns. The high root:shoot ratios of *Ac*, although it could not maintain its normal root production patterns as evident by its relatively low resistance value (Table 2), its high rooting depth and root density were assumed to be helpful mechanisms in survival. They could explain why this species did not show any signs of premature leaf senescence and fall in the autumn season and also why it had relatively high resistance values concerning biomass, stem growth (Table 2), as well as water use [15]. All data supported the assumption that this species was extremely drought resistant [15,19].

With a southern distribution margin, *Ac* originated from a more drought-prone habitat in comparison to *Cb* and *Tc* [35,36]. The extremely potent root system of *Ac* (Tables 2 and 3) and its extremely low hydraulic demand due to low LAI (Table 3) could be due to its origin from a drier habitat [18], which suggested a high drought tolerance of this species, also supported by the drought-tolerance ranking of Niinemets and Valladares [27] (Table 1).

Cb showed low resistance to drought with high losses in the branch and the root biomass and hence a decreasing root:shoot ratio; the latter suggests that under drought, this cultivar does not allocate much carbon to the development of the root system. Instead, with its very densely leafed canopy (Table 2; [14]) it has a high area of hydraulic demand in relation to a low amount of supplying root biomass, which makes it susceptible to drought [13]. This assumption is also in line with the species ranking of Niinemets and Valladares [27] (Table 1), giving the species *Carpinus betulus* the lowest drought-tolerance value among all study species and cultivars.

Under the rainfall exclusion experiment, *Tilia cordata* 'Greenspire' lost branch and root biomass at high rates but could maintain a relatively high root:shoot ratio in combination with a considerable increase in the density of the root system (Table 2). This observation indicates that carbon assimilation was so strongly reduced by drought that there was insufficient assimilation to facilitate its allocation to the entire plant system. Due to the high overall losses in biomass and the extremely early discolouring and fall of leaves (Figure 3), a high susceptibility to drought was assumed for this cultivar. This finding is in line with the results of Stratópoulos [15] who conducted their study at the same location and in the same year and showed that *Tc* had much lower resistance in terms of water use in comparison to *Acer campestre* and *Acer platanoides* and is still considerably lower than that of *Cb*.

4.2. The Role of the Root System in Sustaining Drought

Within the below-ground biomass component, organs perform a range of functions. Coarse roots mainly provide stability, transport, storage, and conduction functions while the fine roots mainly absorb and conduct water and nutrients [37,38]. Generally, plants may increase their soil-to-root or rhizosphere conductance by adjusting their fine-root density, fine root hydraulic conductance, rooting depth, and other root characteristics [13].

Recent research has shown that deep roots can be of pivotal importance to alleviate water stress in several plants [39]. They particularly play the central role for drought tolerance in the tropical and subtropical environments [40]. In our study, we saw a slight increase in the rooting depth of *Tc* under drought conditions (Table 3). Only in *Ac*, both the width and depth of the root system were slightly reduced under decreased soil moisture, while the root biomass of *Ac*-dry was still higher than that of any other species/treatment combination, except for that of its own control group. Moreover, it had the densest root system of all species and cultivars in the dry treatment. In another study [17], it was observed that *Tc* developed its fine roots more in the horizontal than in the vertical direction to cope with drought. Contrarily, we recorded a decrease in the width of the root system (coarse roots) under drought conditions. A possible explanation for this could be that *Tc* did invest less carbon in developing their coarse root system for stability, and rather gave priority to the development of fine roots in order to enhance its water uptake capacity. Such similar phenomenon of reducing coarse roots was also noted for *Ac* and *Cb*.

It should be considered, however, that for growing, particularly the soil conditions in the nursery in the study under which the root systems developed are fundamentally different from those in the real city environment. Here, the underground site conditions usually don't allow unhampered root development making knowledge about genetically determined types of root systems for species and cultivars applicable only to a limited extent. A study on city trees [41] has shown that an important criterion for spatial root development is the existence of loose and permeable soil parts, toward which trees develop their roots. This high influence of the absence and presence of oxygen on the root system architecture leads to extremely untypical growing patterns in the urban environment [41]. It suggests that the spatial extensions measured in this study under almost unlimited rooting space should become less of a concern in species and cultivar choice in comparison to that in the species- and cultivar-specific root system densities and biomass amounts.

5. Conclusions

Predictions suggest a future increase in climate extremes, such as severe drought, due to climate change [1]. Consequently, limited availability of water will be an important cause for tree stress or even complete desiccation that leads to cellular death with significant implications for functions and ecosystem services provided by the trees. The presence or absence of specific structural and functional adjustments and response capacity to cope with the dry conditions may impact species' and cultivars' survival and mortality. In our study, we measured several indexes of three species and cultivars under a controlled experiment and a harvest campaign was applied for the biomass of stem, branch, and root. Valuable information about the root:shoot biomass relations of different tree species and cultivars are provided, and this could be an important selection criterion in species and cultivars choice.

It is assumed that non-lethal droughts can promote drought resilience or the ability to survive droughts because of the acclimation of plant traits [13], future studies should therefore monitor species' performances over several years, including through pre-drought stages and wet periods, where morphological and physiological adaptations clearly manifest themselves according to the respective resource supplies. In an advanced development stage of the trees, this aspect could be achieved by using permanent girth tapes at the stem and root [24] or through retrospective increment core sampling [42].

In this study, *Cb* and *Tc* coped less well with drought than *Ac*. Therefore, they should be rather planted in park-like environments with sufficient water supply, while *Ac* may be more suitable for sites with chronic, severe droughts. Trees should be planted and maintained according to their different strategies and site requirements. For this purpose, we need knowledge about the general growth habit of a species/cultivar, its within-plant carbon partitioning and allocation patterns under changing growing conditions, and the annual growing and wilting cycles, which affect the timing of their physiological processes. In addition, the respective resource supply in the native habitat appears to be a good proxy for drought tolerance, suggesting to progressively plant (non-native) species and cultivars from drier habitats at harsh urban sites [14,15].

We suggest that special attention should be paid to the below-ground biomass and density, which, until date, has received limited research attention. Moreover, sufficient space for the expansion of root growth is necessary to defend drought risk. Future experimental studies are supposed to reduce or even close the disparity in the knowledge between the below-ground processes in comparison to the above-ground processes, which are until date, reasonably better understood. Corresponding knowledge is expected to provide important insights for urban greenspace planning and management, particularly for the selection of suitable tree species and cultivars.

References

1. IPCC. Climate Change 2013: The Physical Science Basis. In *Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*; Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M., Eds.; Cambridge University Press: Cambridge, UK; New York, NY, USA, 2013.

2. Roloff, A.R. Stadt-und Straßenbäume der Zukunft—Welche Arten sind geeignet? *Forstwiss Beitr Tharandt Beih* **2013**, *14*, 173–187.

3.　Oleson, K.W.; Bonan, G.B.; Feddema, J. Effects of white roofs on urban temperature in a global climate model. *Geophys. Res. Lett.* **2010**, 37. [CrossRef]

4.　Sailor, D.J. A review of methods for estimating anthropogenic heat and moisture emissions in the urban environment. *Int. J. Climatol.* **2011**, *31*, 189–199. [CrossRef]

5.　Stone, B.; Vargo, J.; Habeeb, D. Managing climate change in cities: Will climate action plans work? *Landsc. Urban Plan.* **2012**, *107*, 263–271. [CrossRef]

6.　Moser, A.; Rahman, M.A.; Pretzsch, H.; Pauleit, S.; Rötzer, T. Inter- and intraannual growth patterns of urban small-leaved lime (Tilia cordata mill.) at two public squares with contrasting microclimatic conditions. *Int. J. Biometeorol.* **2017**, *61*, 1095–1107. [CrossRef] [PubMed]

7.　Pretzsch, H.; Biber, P.; Uhl, E.; Dahlhausen, J.; Schütze, G.; Perkins, D.; Rötzer, T.; Caldentey, J.; Koike, T.; van Con, T.; et al. Climate change accelerates growth of urban trees in metropolises worldwide. *Sci. Rep.* **2017**, *7*, 15403. [CrossRef] [PubMed]

8.　Rahman, M.A.; Moser, A.; Rötzer, T.; Pauleit, S. Microclimatic differences and their influence on transpirational cooling of *Tilia cordata* in two contrasting street canyons in Munich, Germany. *Agric. For. Meteorol.* **2017**, *232*, 443–456. [CrossRef]

9.　Nowak, D.J.; Crane, D.E.; Stevens, J.C. Air pollution removal by urban trees and shrubs in the United States. *Urban For. Urban Green.* **2006**, *4*, 115–123. [CrossRef]

10.　Armson, D. The Effect of Trees and Grass on the Thermal and Hydrological Performance of an Urban Area. Ph.D. Thesis, University of Manchester, Manchester, UK, 2012.

11.　Nowak, D.J.; Greenfield, E.J.; Hoehn, R.E.; Lagpoint, E. Carbon storage and sequestration by trees in urban and community areas of the United States. *Environ. Pollut.* **2013**, *178*, 229–236. [CrossRef]

12.　Rahman, M.A.; Moser, A.; Rötzer, T.; Pauleit, S. Within canopy temperature differences and cooling ability of *Tilia cordata* trees grown in urban conditions. *Build. Environ.* **2017**, *114*, 118–128. [CrossRef]

13.　McDowell, N.; Pockman, W.T.; Allen, C.D.; Breshears, D.D.; Cobb, N.; Kolb, T.; Plaut, J.; Sperry, J.; West, A.; Williams, D.G.; et al. Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? *New Phytol.* **2008**, *178*, 719–739. [CrossRef] [PubMed]

14.　Stratópoulos, L.M.F.; Duthweiler, S.; Häberle, K.-H.; Pauleit, S. Effect of native habitat on the cooling ability of six nursery-grown tree species and cultivars for future roadside plantings. *Urban For. Urban Green.* **2018**, *30*, 37–45. [CrossRef]

15.　Stratópoulos, L.M.F.; Zhang, C.; Duthweiler, S.; Häberle, K.-H.; Rötzer, T.; Xu, C.; Pauleit, S. Tree species from two contrasting habitats for use in harsh urban environments respond differently to extreme drought. *Int. J. Biometeorol.* **2019**, *63*, 197–208. [CrossRef] [PubMed]

16.　Choat, B.; Jansen, S.; Brodribb, T.J.; Cochard, H.; Delzon, S.; Bhaskar, R.; Bucci, S.J.; Field, T.S.; Gleason, S.M.; Hacke, U.G.; et al. Global convergence in the vulnerability of forests to drought. *Nature* **2012**, *491*, 752–755. [CrossRef] [PubMed]

17.　Zhang, C.; Stratopoulos, L.M.F.; Rötzer, T.; Xu, C.; Pretzsch, H. Development of fine-root biomass in response to drought stress of two contrasting urban tree species. under review.

18.　Mokany, K.; Raison, R.J.; Prokushkin, A.S. Critical analysis of root:shoot ratios in terrestrial biomes. *Glob. Chang. Biol.* **2006**, *12*, 84–96. [CrossRef]

19.　Kunz, J.; Räder, A.; Bauhus, J. Effects of drought and rewetting on growth and gas exchange of minor European broadleaved tree species. *Forests* **2016**, *7*, 239. [CrossRef]

20.　Sjöman, H.; Nielsen, A.B.; Pauleit, S.; Olsson, M. Habitat Studies Identifying Potential Trees for Urban Paved Environments: A Case Study from Qinling Mt., China. *Arboric. Urban For.* **2010**, *36*, 261–271.

21.　Sjöman, H.; Gunnarsson, A.; Pauleit, S.; von Bothmer, R. Selection Approach of Urban Trees for Inner-city Environments: Learning from Nature. *Arboric. Urban For.* **2012**, *38*, 194–204.

22.　Gillner, S.; Vogt, J.; Tharang, A.; Dettmann, S.; Roloff, A. Role of street trees in mitigating effects of heat and drought at highly sealed urban sites. *Landsc. Urban Plan.* **2015**, *143*, 33–42. [CrossRef]

23.　Dahlhausen, J.; Uhl, E.; Heym, M.; Biber, P.; Ventura, M.; Panzacchi, P.; Tonon, G.; Horváth, T.; Pretzsch, H. Stand density sensitive biomass functions for young oak trees at four different European sites. *Trees* **2017**, *31*, 1811–1826. [CrossRef]

24.　Rötzer, T.; Biber, P.; Moser, A.; Schäfer, C.; Pretzsch, H. Stem and root diameter growth of European beech and Norway spruce under extreme drought. *For. Ecol. Manag.* **2017**, *406*, 184–195. [CrossRef]

25.　DWD. 2018. Available online: https://www.dwd.de (accessed on 15 March 2018).

26. BGR. *Bodenkundliche Kartieranleitung*; E. Schweizerbart'sche: Hannover, Germany, 2005.

27. Niinemets, Ü.; Valladares, F. Tolerance to shade, drought, and water logging of temperate northern hemisphere trees and shrubs. *Ecol. Monogr.* **2006**, *76*, 521–547. [CrossRef]

28. Zhang, C.; Stratopoulos, L.M.F.; Pretzsch, H.; Rotzer, T. How Do Tilia Cordata Greenspire Trees Cope with Drought Stress Regarding Their Biomass Allocation and Ecosystem Services? *Forests* **2019**, *10*, 676. [CrossRef]

29. Biologische Bundesanstalt für Land- und Forstwirtschaft. Available online: http://www.agrometeo.ch/sites/default/files/u10/bbch-skala_deutsch.pdf (accessed on 18 August 2018).

30. Miller, J.B. A formula for average foliage density. *Aust. J. Bot.* **1967**, *15*, 141–144. [CrossRef]

31. Welles, J.M.; Norman, J.M. Instrument for indirect measurement of canopy architecture. *Agron. J.* **1991**, *83*, 818–825. [CrossRef]

32. Hotaling, N.A.; Bharti, K.; Kriel, H.; Simon, C.G., Jr. DiameterJ: A validated open source nanofiber diameter measurement tool. *Biomaterials* **2015**, *61*, 327–338. [CrossRef] [PubMed]

33. *R: A Language and Environment for Statistical Computing*; R Core Team: Vienna, Austria, 2014.

34. *ArcGIS*, version 10.2.1; Esri: Redlands, CA, USA, 2014.

35. Kiermeier, P. *Die Lebensbereiche der Gehölze eingeteilt nach dem Kennziffernsystem*; Grün ist Leben: Pinneberg, Germany, 1995.

36. Roloff, A.R.; Bärtels, A. *Flora der Gehölze—Bestimmung, Eigenschaften Verwendung*; Ulmer Verlag: Stuttgart, Germany, 2008.

37. Jackson, R.B.; Mooney, H.A.; Schulze, E.D. A global budget for fine root biomass, surface area, and nutrient contents. *Proc. Natl. Acad. Sci. USA* **1997**, *94*, 7362–7366. [CrossRef]

38. Reubens, B.; Poesen, J.; Danjon, F. The role of fine and coarse roots in shallow slope stability and soil erosion control with a focus on root system architecture: A review. *Trees* **2007**, *21*, 385–402. [CrossRef]

39. Gewin, V. Food: An underground revolution. *Nat. News* **2010**, *466*, 552–553. [CrossRef]

40. Pierret, A.; Maeght, J.L.; Clément, C. Understanding deep roots and their functions in ecosystems: An advocacy for more unconventional research. *Ann. Bot.* **2016**, *118*, 621–635. [CrossRef]

41. Reichwein, S. Baumwurzeln unter Verkehrsflächen. Untersuchungen zu Schäden an Verkehrsflächen durch Baumwurzeln und Ansätze zur Schadensbehebung und Schadensvermeidung. Ph.D. Thesis, University of Hannover, Hannover, Germany, 2002.

42. Pretzsch, H.; Uhl, E.; Biber, P.; Schütze, G.; Coates, K.D. Change of allometry between coarse root and shoot of Lodgepole pine (Pinus contorta DOUGL. ex. LOUD) along a stress gradient in the sub-boreal forest zone of British Columbia. *Scand. J. For. Res.* **2012**, *27*, 532–544. [CrossRef]