

# Tree water relations of mature oaks in southwest Germany under extreme drought stress in summer 2018

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## ABSTRACT

Mature oak stands of different tree height at four sandy valley river sites (*Quercus robur*) and one south-exposed schist slope (*Qu. petraea*) in the middle Rhine and lower Main valley were studied from early summer 2017 (normal wet year) until the end of 2018 (extremely hot and dry year). Tree water relations ( $\Psi_{pd}$ , RWC, sap flow rates) were monitored together with soil water relations, LAI and leaf chl content. In two sandy sites with presumed continuous capillary water access from the groundwater aquifer, sap flow rates of the large trees (30 m) and estimated canopy conductance decreased to about 50% of the maximum value in the course of summer 2018, but recovered in autumn. At two other sites, with smaller trees (14–24 m) and presumed interrupted capillary water access during mid-summer 2018, sap flow rates and canopy conductance broke down completely and trees shed a large proportion of leaves in summer. In one of these sites,  $\Psi_{pd}$  decreased (reversibly) to -4 MPa, one of the lowest values reported in the literature for central Europe, and tree damage resulted not only in extreme leaf shedding, but also in susceptibility to uprooting (in 2 out of 5 measured trees) by thunderstorm gusts in autumn 2018. At the schist slope site, where oaks reached the lowest height and stand density of all sites, sap flow rates remained similar to the values found at the presumed capillary-water supplied sandy sites, indicating access to rock fissure water even at the peak of the drought period. Our findings corroborate the prediction from vegetation modelling that several *Qu. robur* stands in the Rhine-Main valleys will be prone to severe forest dieback in the forthcoming decades.

## 1. Introduction

On sandy river terrace soils and shallow soils on south-exposed slopes in the Rhine and Main valleys in South Hesse, water supply is a major constraint for traditional forestry use. Especially after the extreme dry and hot years 2003, 2018 and 2019, forest stands all over Central Europe experienced unprecedented crown and whole-tree dieback events, both in coniferous and deciduous stands (Schuldt et al., 2020; Walthert et al., 2021; Rohner et al., 2021), whereas the 2017 heat-wave in southern Europe resulted in (mostly reversible) defoliation of beech and deciduous oaks in Tuscany (Pollastrini et al. 2019). Such weather extremes are likely to increase in the course of climate change (Schär et al., 2004; Kirtman et al., 2013; Jacob et al., 2014) and the severity of damage strongly depends on stand characteristics concerning water availability (Rita et al. 2020, Skiadaresis et al., 2019). In this context, groundwater access of oak-dominated forest types in European floodplain forests has been an important buffer against drought effects

in the past (Levanic et al., 2011; Skiadaresis et al., 2019; Stojanović et al., 2015). However, with an increase of water extraction especially in the big river valleys in Central Europe for agricultural, industrial and drinking water purposes in the vicinities of urban centres, many of these (established) forests lost direct groundwater access after the 1940s. Since older *Qu. robur* trees probably cannot adopt their root system to changing ground water supply (Thomas and Hartmann 1992), *Qu. robur* floodplain forests are especially prone to damage by combinations of decreased groundwater levels and increasing heat and drought waves, which are considered a major factor in the European-wide observed so-called “acute oak decline” (Thomas et al. 2003, Thomas 2008, Skiadaresis et al., 2019). This multi-factorial phenomenon with combined effects of abiotic and biotic stressors does not only affect *Qu. robur* floodplain forests, but also other oak stands across Europe, including *Qu. petraea* in France and deciduous and even evergreen oaks in the Mediterranean basin (Brasier et al., 1993; Eaton et al., 2016, Führer, 1988, Ragazzi et al., 1998).

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### Abbreviations

BA	basal area (basal area stem [dm <sup>2</sup> ]/ground area [m <sup>2</sup> ])
DBH	diameter at breast height (130 cm)
DOY	day of the year
dT	temperature difference between heated and reference probe
dT <sub>max</sub>	maximum temperature difference between heated and reference probe when sap flux = 0
DW	dry weight
DWD	Deutscher Wetterdienst (German Meteorological Survey), Offenbach, Germany
E	stand transpiration
F <sub>D</sub>	sap flux density [L * dm <sup>-2</sup> <sub>sapwood</sub> * h <sup>-1</sup> ]
FSA	relative sapwood area [dm <sup>2</sup> <sub>sapwood</sub> * m <sup>-2</sup> <sub>ground area</sub> ]
FW	fresh weight
g <sub>c</sub>	canopy conductance [mm * s <sup>-1</sup> ]
G <sub>V</sub>	gas constant for water vapour
HLUG (now HLNUG)	Hessian Agency for (Nature Conservation,) Environment and Geology, Wiesbaden, Germany
k	dimensionless “flow index” (Oishi et al., 2016)
LA	Lampertheim
LO	Lorchhausen
Ψ <sub>m</sub>	soil water potential
Ψ <sub>PD</sub>	predawn leaf water potential
pF	water content of soil (dimension less)
ρ <sub>w</sub>	density of water
RU	Rüsselsheim
RWC	relative leaf water content
SW	Frankfurt-Schwanheim
T	temperature
TDP	thermal dissipation probe
TW	turgor weight
VPD	Vapour pressure deficit

In the Rhine and Main valleys, several forest stands have recently been devastated, with the percentage of damaged trees of all kind of species exceeding 90% locally (Frankfurt City forest, 2019, as reported by the City Council –unpublished–). However, this was not a new phenomenon: in groundwater-depleted oak stands, damage to existing oak forests by summer drought periods has been recorded previously for many years, especially after the extreme 2003 drought (HMULV 2006). Apart from mortality counts, tree fitness of the live canopy can be monitored by methods describing crown damage (with damage classes) and crown cover (LAI; Pearse et al., 2015).

To address potential solutions for maintaining forest cover in these areas, it is essential to understand the water status of the trees in question. Since summer droughts for a few weeks occurred frequently during the past years in these stands (own observations), we aimed at correlating hydrological soil data, weather data and physiological data on tree water status for a gradient of mature oak (*Qu. robur*) stands (> 80 years) on sandy soil, ranging from a relatively dense forest (LA2) with trees of roughly 30 m height, via a drought- and storm-damaged stand of trees of similar size (LA1) to stands supposedly experiencing more drought, with tree sizes of 14–25 m (SW) and 14 m (RU), respectively. The central purpose of this study was to experimentally verify or deny groundwater access of individual trees by physiological measurements on leaves and stems. Monitoring tree sap flow has been established as a valuable technique to describe the water status of trees as the underlying stress factor

during summer dry spells, and to assess stand transpiration by upscaling (e.g. Granier and Bréda 1996; Wullschlegler et al., 2001; Lundblad and Lindroth 2002; Grossiord et al., 2014). Since the four sandy stands, in principle, experienced similar precipitation and showed similar groundwater levels (−3.7 to −4.2 m in summer, Suppl. Fig. S1), we installed sap-flow sensors for long-term monitoring trunk water transport in order to assess whether water accessibility can explain the different growth of the trees, as evident from their heights. The selected *Qu. robur* stands were further compared to a ca 40-year old *Qu. petraea* stand (ca 10 m height) on a steep, SW exposed schist rock slope, with no groundwater access. We started our measurements in early summer 2017, with normal precipitation patterns, and kept recording during 2018, when an unprecedented heat and drought wave hit Central Europe. In vegetation modelling, usually standardized values are used for simulating water fluxes through tree canopies, often derived from gas flux measurements (CO<sub>2</sub>, water vapour) taken under favourable growth situations, and assuming minimum canopy conductances of 0.3 – 0.5 mm/s (e.g. established, healthy forests with good water supply: LPJ-GUESS: Smith et al., 2001, Hickler et al., 2012). However, little data are available in the literature for marginal stands at the dry edges of distribution areas. Therefore, from the sap flow data, we also estimated stand canopy conductance and its dependence on leaf development and soil water availability to obtain experimental evidence for a future better parametrizing of existing vegetation models.

In particular, this contribution addresses the following questions:

- (1) Do the selected oak stands, with different tree heights in the same mesoclimate differ in water transport?
- (2) Can we corroborate ground / capillary water access of different oak stands by sap flow measurements?
- (3) Does water supply affect canopy conductance, estimated from sap flow vs vapour pressure deficit plots?

## 2. Materials and methods

### 2.1. Monitoring sites and trees

The monitored sites are located in the communal forests of the cities of Rüsselsheim (RU: N49°57'11.1" E8°24'52.6") and Frankfurt-Schwanheim (SW: N50°04'23.8" E8°34'07.9"), in the Hessian state forest near Lampertheim. (LA1: N49°35'05.3" E8°34'40.0" & LA2: N49°35'06.2" E8°33'57.0"), and on a former wine yard close to the village Lorchhausen (LO: N50°03'16.4" E7°47'06.7").

The RU site is situated on an eolian sand dune, with a semi-open *Quercus robur* L. and *Pinus sylvestris* L. stand. The area has a history of hog-feeding in the 17th/18th century, with a few remnant old oaks. In the 20th century, plantation of *P. sylvestris* occurred, but during world war II and the following decades, management efforts were reduced and regrowth of *Q. robur* occurred. The monitored oaks were ca. 80–85 years old with a diameter at breast height (DBH) between 29.3 and 39.5 cm and a height from 11.5 to 14.5 m. They filled a basal area (BA) of approximately 0.154 dm<sup>2</sup> m<sup>-2</sup> between pines (BA 0,024 dm<sup>2</sup> m<sup>-2</sup>) and a scattered shrub layer of blackberry.

The site in SW is characterized by fluvial sand of the Southern Middle Terrace of the Main Valley. The monitored *Q. robur* trees were 80–100-years old, with a DBH between 28.9 and 63.7 cm and height from 14.0 to 24.5 m. The BA of the oaks was 0.178 dm<sup>2</sup> m<sup>-2</sup> with a single pine (0.047 dm<sup>2</sup> m<sup>-2</sup>) and some young oaks (0.006 dm<sup>2</sup> m<sup>-2</sup>) in between. Traditionally, the area was used for hog-feeding as in RU, and remnant old oaks (> 200 years) can be found in the vicinity.

In the forest near Lampertheim there are two different sites (LA1+2) close together on the same fluvial sandy-soil of the Rhine. Since 1964, the region's groundwater table has been reduced from previous −2.2 to −5.5 m depth at the end of the 1970s by water extraction for drinking water and for irrigation of agriculture. As a consequence, the availability of water for the vegetation decreased and the forest in the area (Hessian

Ried) became weaker and thinner. Since the 2000s, attempts have been made to stabilize the level around - 3.5 m (Jacobsen and Ullrich 2012). The LA1 oak stand is characterized by a perforated vegetation canopy cover of *Quercus robur* L (198 years old, DBH 65.9 - 102 cm, 29.5 - 34.5 m height, BA 0.425 dm<sup>2</sup> m<sup>-2</sup>) mixed with semi-adult *Fagus sylvatica* L. (BA 0.039 dm<sup>2</sup> m<sup>-2</sup>), young *Acer spec.* (BA 0.026 dm<sup>2</sup> m<sup>-2</sup>) and a moderate scrub layer between. In 2007 the storm 'Kyrill' hit this oak stand and opened the canopy. The crowns of the remaining oaks are in an exposed position above the younger layer and show an advanced degradation state. The LA2 site is a planted *Quercus robur* L. stand (120 years old, DBH 44.6-58.9 cm, 27.5 - 29.5 m height, BA 0.290 dm<sup>2</sup> m<sup>-2</sup>) mixed with semi-adult *F. sylvatica* L. (BA 0.075 dm<sup>2</sup> m<sup>-2</sup>), 880 m west of LA1, and is managed for forestry purposes. The canopy is relatively closed and a scrub layer is missing.

The soil properties for RU, SW & LA have been described in Koller et al. (2014). Data for the subsoil layers have been provided by Hessisches Landesamt für Umwelt und Geologie, Wiesbaden, Germany. At LA, different sand layers reached down to about 6.4 m; below this level, sand was combined with gravel. At SW, sand layers went down to 3.45 m, after which gravel and gravel/sand layers were found down to 9.10 m. At RU, no well was drilled, but a hole was excavated and the upper 2 m of the ground consisted of fine sand. At the closest by hydrogeological well (i.e. 350 m southwest of the oak stand), which is located at a natural pond above a clay lense, below the clay layer 3,75 m of sand were found and below this, 3.85 m of scree / sand mixture.

In LO, the closely related oak species *Quercus petraea* Matt. (Liebl.) (40 years old, DBH 21.3 - 34,1 cm, 9.5-12.0 m height, BA 0.166 dm<sup>2</sup> m<sup>-2</sup>) inhabits, together with a wild cherry tree (BA 0.006 dm<sup>2</sup> m<sup>-2</sup>) and a mountain ash specimen (BA 0,003 dm<sup>2</sup> m<sup>-2</sup>), a south-exposed former vineyard, on a sandy schist soil without humus or scrub layer. The slope has a gradient of 61° and schist is present on the surface in different stages of degradation. The site is surrounded by autochthonous *Qu. petraea.* / *Acer monspessulanum* L forest, but trees here could not be probed due to conservation restrictions.

## 2.2. Meteorological data

All meteorological and soil water conditions were recorded by iMetos SMT280 climate stations (Pessl Instruments, Weiz, Austria) on free areas close to the studied oaks. The soil moisture was measured with a water mark sensor [soil water potential ( $\Psi_m$ ) range of the sensors at RU, FR & LA: 0 to -200, at LO: 0 to -250 hPa] at a depth of 100 cm. For better comparability, the values were converted to the dimensionless pF value (Hartge and Horn 2009)

$$pF = \log_{10} \left| \frac{\Psi_m}{hPa} \right| \quad (1)$$

Based on the recorded mean daily air temperature ( $T_{med}$ ), the beginning and end of the growing season for higher plants in the temperate zone was identified by  $T_{med} \geq 10$  °C on five consecutive days in spring and  $T_{med} \leq 10$  °C in autumn (Winkler 1980). Vapour pressure deficit (VPD) was calculated from air temperature and dew point according to Allen (2002). The ground water table data were monitored by ground water stations close to the oak stands (distances: RU 350 m, SW 90 m, LA1 130 m and LA2 360 m), made available by the (formerly) Hessisches Landesamt für Umwelt und Geologie (HLUG) and adjusted to the elevated ground level of the stand if needed. Due to the geological conditions of the LO site, no groundwater data were available. Additional meteorological data were obtained from DWD (Deutscher Wetterdienst, Offenbach) and are indicated where necessary.

## 2.3. Crown cover development and chlorophyll content

Crown cover development was measured on eight days throughout the vegetation period, with a SunScan Probe SS1-RL4 with radio receiver links to a BF5-RL4 Sunshine Sensor as uncovered reference (Delta-T Devices Ltd, Cambridge, UK). Data were acquired with SunData software

(version 1.02R, Peak Design Ltd, Derbyshire, UK) in LAI units and we report means of all trees with integrative measurements per tree (in east, north-east, north, north-west and west direction at 0,5 m distance from the trunk). For background cleaning (branches and stem), a single measurement was performed in December 2017/January 2018 after leaf abscission and subtracted from the values of the vegetation phase.

The development of the relative Chlorophyll content was assessed with a SPAD-502 chlorophyll metre (Konica Minolta, Munich, Germany) on ten days during 2018. Due to the accessibility of leaves, the measurements could only be carried out within the stands of RU, SW and LO. For each tree, five undamaged and fully developed leaves from branches with southern orientation in heights of 2,0-4.5 m were selected and an average value of 6-8 single measurements (depending on leaf size) were recorded. This results in 25 tested leaves per stand. The number of replicates in RU decreased to 15 after the wind felling in autumn 2018.

## 2.4. Water status of the trees

### 2.4.1. Relative leaf water content (RWC) and predawn water potential ( $\Psi_{pd}$ )

In 2018, five south exposed leaves per tree, previously used for the SPAD measurements were cut predawn from the trees together with the branches and brought to the laboratory for the determination of RWC. They were transported in airtight plastic bags on ice. The RWC was determined according to Smart and Bingham (1974) by using the whole leaves. After cutting off the petiole and drying the leaf surface if necessary, the fresh weight (FW) was recorded. The time to achieve full turgidity and to measure the turgor weight (TW) was at least 24 h (without light in a wet tissue in a plastic bag). The leaves were then dried at 90 °C until constant weight for the determination of dry weight (DW) was reached. RWC was then calculated as

$$RWC(\%) = (FW - DW) * 100 / (TW - DW) \quad (2)$$

The predawn (branch) water potential ( $\Psi_{pd}$ ) was measured with a Scholander pressure chamber (SKPM 1400 pressure chamber, SKYE Instruments, Powys, UK), using five north-facing branches per tree (heights of 2,0-4.5 m), one to three hours before sunrise. The monitoring periods in RU and SW started in summer 2017 (DOY 158/171) and again in spring 2018 (DOY 81). In LO the measurements commenced in spring 2018 (DOY 106). The records always ended after leaf shedding. A group of five dominant trees at each site were selected by their vitality, distance to other major trees and (if possible) sapwood thickness above 20 mm. The sapwood thickness was determined at breast height by extracting wood cores from the northern and the southern side of each tree, one each, with a Pressler increment borer (SUUNTO 2,5 mm, IML-System GmbH, Wiesloch, Germany). The wood core cylinder was cut longitudinally and indicator dye (Methyl-Orange, 0,1%) was applied to identify the sapwood part. Sapwood thickness was measured by using a digital caliper ( $\pm 0,05$  mm) under the magnification of a binocular. For estimating the sapwood area of each tree, the mean value from the two cores per stem were used. After completion of the sap flow measurements, further samples of the sapwood were taken in the immediate vicinity of the sensor area to verify the previous assumptions about the layer thickness.

### 2.4.2. Sap flow measurements

To monitor the water status of the oaks, two 20 mm long sensors of thermal dissipation probe (TDP, Ambio-Tec Umweltmesstechnik & Handel, Osnabrück, Germany) were installed under the bark and cambium on the northern side of each measured tree, at around 1.3 m above soil level (heater probe) with a 12.5 cm vertical spacing between the probes. To protect the sensors from moisture and rapid temperature changes, we covered the sensors with a plastic seal and shielded them with a thin layer of aluminium-covered polystyrene. The measurement interval was 30 min and data were recorded automatically with a CR800 data logger (Campbell Scientific, Logan, USA). Continuous recording over the whole

**Table 1**  
Estimated canopy conductance, as determined from relative sapwood area per m<sup>2</sup> canopy area and the initial slopes of the hourly sap-flow values vs. VPD plots (Fig. S5, Table S3). Rates at LA2 are underestimates, since the canopy is denser and VPD across the leaf surface thus is overestimated, cf. Section 2.5.

Parameter	Period	RU	SW	LA1	LA2	LO
BA*FSA (dm <sup>2</sup> /m <sup>2</sup> )		0.031	0.036	0.049	0.047	0.009
dE/dVPD <sub>max</sub> (l/dm <sup>2</sup> h kPa)	July 2017	0.169	0.183	0.230	0.227	ND
	June 2018	0.135	0.165	0.203	0.173	0.131
	July/Aug 2018	0.008	0.027	0.097	0.085	0.006
g <sub>cest</sub> max (mm/s)	July 2017	0.393	0.494	0.845	0.800	ND
	June 2018	0.314	0.445	0.746	0.610	0.088
	July/Aug 2018	0.019	0.073	0.356	0.300	0.004

period was realised by connecting the batteries to solar panels. Prior to measuring, the TDP heating element was turned on for five minutes by 0.2 W. Due to the insufficient thickness of the sapwood in LO, the radial distribution correction according to Clearwater et al. (1999) was carried out here.

Technical problems with individual sensors and damaging wildlife activity during the vegetation periods occurred at all sites for various intervals, reducing, in some cases, the numbers of biological replicates and are summarized in Suppl. Table 2. However, all data presented were means of at least 3 trees at each point of time.

Sap flux density ( $F_D$ ) was calculated according to (Granier 1987) and (Grossiord et al., 2014) as:

$$F_D = 4.28 \left( \frac{dT_{max}}{dT} - 1 \right)^{1.231} \left[ L * dm_{sapwood}^{-2} * h^{-1} \right] \quad (3)$$

The determination of  $dT_{max}$ , the maximum temperature difference during zero sap flow, was performed with the sap flow software BASELINER 4.0 (Oishi et al., 2016). The threshold parameters to identify zero-flow condition between midnight and 6 a.m. were radiation = 0 W/m<sup>2</sup>; VPD ≤ 0,09 kPa, dT-variations coefficient ≤ 0,005 at two-hour-intervals. Based on this, we calculated the hourly [ $L * dm_{sapwood}^{-2} * h^{-1}$ ] and by accumulation the daily [ $L * dm_{sapwood}^{-2} * day^{-1}$ ] sap flux density of each tree ( $F_{Dtree}$ ) and finally the mean sap flux density for the whole sapwood area of each site ( $F_{Dmean}$ ).

## 2.5. Canopy conductance

From the slope of the linear regression of the stand evapotranspiration at VPD < 1 kPa we estimated the canopy conductance ( $g_c$ ) according to Hogg and Hurdle (1997): First, the half-hourly  $F_D$  and corresponding VPD-values during daytime (determined by a threshold value for solar radiation of ≥10 W\*m<sup>-2</sup>) were recorded. Stand transpiration ( $E$ ) can then be calculated as a function of  $F_D$ , BA and fraction of basal tree area occupied by sapwood (FSA), determined from radial increment wood cores (i.e.  $E = F_D * BA * FSA$ ). If the forest situation includes high aerodynamic conductance, as it is the case in open stands (like in LO, SW, RU and LA1), the VPD of the ambient air, as calculated from relative atmospheric humidity and temperature, is close to the vapour pressure gradient across the stomata (Hogg and Hurdle 1997). Therefore, in a second step,  $g_c$  [ $mm s^{-1}$ ] can then be estimated as  $k * \Delta E / \Delta VPD$ , with  $\Delta E / \Delta VPD$  being the (initial) slope of the E/VPD curve (taken at values of  $V < 1$  kPa and converted from [ $L / dm^2 * h * kPa$ ] to [ $mm / s * kPa$ ]) and  $k = \rho_w * G_v * T$  ( $\rho_w$ : density of water,  $G_v$ : gas constant for water vapour;  $T$ : temperature in °K). At 20 °C,  $k$  equals  $135 * 10^3$  kPa; However, Steppe et al. (2010) found an underestimation of actual sap flux density by 60% using the thermal dissipation method. Similarly, Wilson et al. (2001) reported a 50% underestimation of stand evapotranspiration by sap flow measurements when comparing long-scale data sets obtained by sap-flow, eddy covariance and river catchment water balance data. To correct for this empirical discrepancy between the different methods, we introduce a factor of 2 for converting  $F_D$ -derived values to estimated (more realistic) stand evapotranspiration, similarly

to the procedure used by Hogg and Hurdle (1997), who introduced a factor of 2 to correct for “wounding effects” to convert the measured  $F_D$  values to (realistic) canopy conductance. Hence,

$$g_{cest} [mm/s] = 2 * 135 * 10^3 kPa * BA \left[ \frac{m_{sapwood}^2}{m_{treearea}^2} \right] * FSA \left[ \frac{m_{treearea}^2}{m_{area}^2} \right] * \Delta F_D / \Delta VPD \left[ \frac{L}{dm_{sapwood}^2} \right] * h * kPa * [1h/3600s] * [100mm/dm] \quad (4)$$

It should be taken into account, that in a dense forest (like LA2), this equation implies an overestimation of the real  $\Delta VPD$  and, thus, an underestimation of  $g_c$ .

To divide (to split up) the resulting scatter of the entire observation period, different hydrological states during the year, characterised by physiological parameters like leaf development and senescence, phases of meteorological events and coherent soil condition (temperature, drought-phase and changes in soil moisture) were used to define specific timeframes for periodically analysis (see Suppl. Fig. S5A+B and Table 1).

## 3. Results

### 3.1. Meteorological data

Summer 2017 was moderately warm (17,18 vs. the 17,45 °C average for 1981–2010 in May–September, DWD, Frankfurt airport) with temperature maxima beyond 37 °C and moderately wet throughout the Rhine-Main region. Only April and June revealed a moderately negative climatic water balance (i.e. precipitation minus evapotranspiration), except for LA (negative climatic water balance only in April), and the annual precipitation was close to the long-year average. In contrast, 2018 was much warmer (average May–September: 19,2 °C at Frankfurt airport), characterized by extreme summer heat and drought, very similar to the historical heat and drought year 2003. Maximum temperatures in the experimental sites exceeded 40 °C in LA and 41 °C in SW and RU and broke all-time records, except for LO (36,9 °C), and all months of the growing season showed negative climatic water balance with one exception only (April 2018 in SW). At Frankfurt airport, growing season precipitation was only 164 mm vs an average of 373 mm (DWD), resulting in negative climatic water balances of – 127 (SW) to – 278 mm (LO, LA). The full data sets are compiled in supplementary Figures S1–3 and Tables S1–2. The negative climatic water balances resulted in groundwater tables declining massively by 0.3 to 0.8 m below winter levels in the course of summer and autumn (Figure S4) and a decrease of soil moisture (1 m depth) to the lowest values which the sensors would record, i.e. pF 3.3 at RU, SW and LA and 3.4 at LO (Fig. S2), or outside the sensor range, for several weeks.

### 3.2. Crown cover development and chlorophyll content

In spring 2018, leaf development was normal, due to sufficient water availability from a wet winter. By DOY 160 (begin June), maximum crown cover and by mid-June maximum chlorophyll contents were

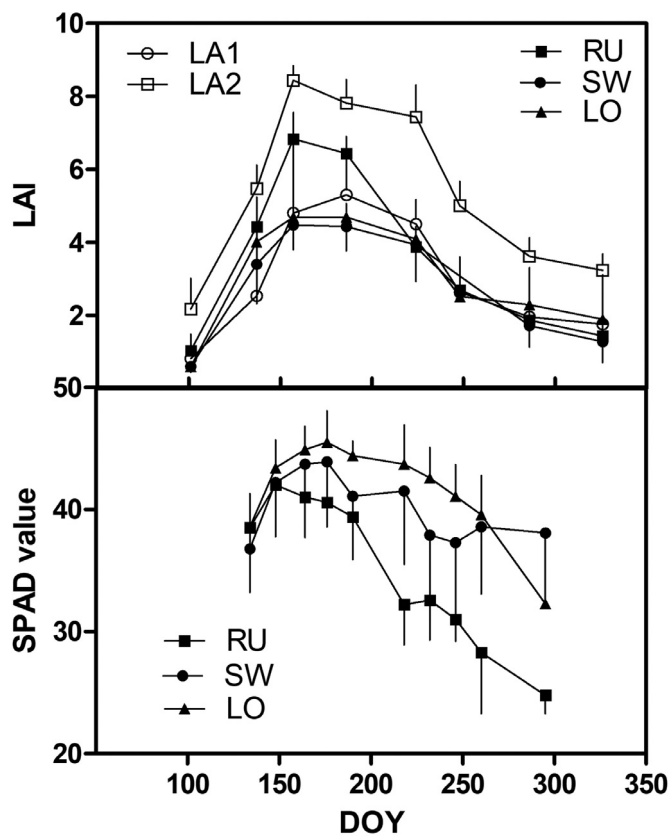


Fig. 1. Leaf Area Index (LAI) and chlorophyll content (relative SPAD values) in the course of the vegetation period 2018. Means [ $n = 25$  (SPAD; after DOY 250: only 15 at RU), 5 (LAI; after DOY 250: only 3 at RU)], SD indicated.

reached (Fig. 1). The highest LAI values were observed at the LA2 site, followed by RU. However, at the RU site, significant chl loss occurred after DOY 220 (begin August), coinciding with significant leaf shedding at this site. It should be noted in this context, that on September 23th, a large proportion of the mature oak and pine trees, including two of the five monitored oaks, were uprooted at the site by wind gusts of a thunderstorm with maximum wind speeds in the region of 22–23 m/s (10 m above ground, weather stations of DWD at Frankfurt airport, east of the site and at Geisenheim, west of the site). Due to a technical problem (too low zenith angle of the sun at the time of measurement), LAI data for SW on DOY 248 was omitted in Fig. 1. Both sites at LA also showed severe leaf shedding during August.

### 3.3. Relative leaf water content (RWC) and predawn (branch) water potential ( $\Psi_{PD}$ )

$\Psi_{PD}$  and leaf RWC decreased from mid-June onwards gradually, until minimum values were reached begin August at RU, SW and LO (Fig. 2). At RU, an extremely low  $\Psi_{PD}$  of -4 MPa was recorded in August. At SW (and less so at RU), transitory partial recoveries were observed after DOY 220 (begin August), following some minor precipitation events (cf. Fig. S2). After DOY 260 (mid-September), a strong rainfall event occurred throughout the observation area and nearly full recovery set in at RU and SW, with only partial recovery of  $\Psi_{PD}$  at LO.

### 3.4. Sap flow and estimated canopy conductance

Fig. 3 depicts the annual course of daily water transport in the stems of mature oaks, compared to data from July-Dec 2017. The courses followed typical patterns with intermittent maxima, coinciding with days characterized by high VPD and minima (wet days, low VPD) (cf. Fig.

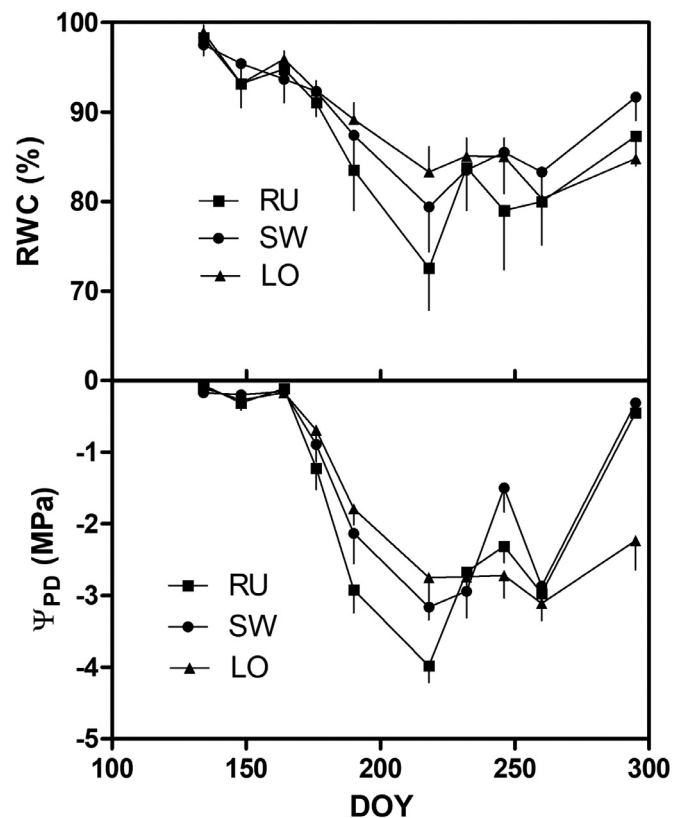


Fig. 2. Relative leaf water content (% of fully water saturated leaves) and predawn branch water potentials in the course of the vegetation period 2018. Means [ $n = 25$  (RWC; after DOY 250: only 15 at RU), 5 ( $\Psi_{PD}$ ; after DOY 250: only 3 at RU)], SD indicated.

S4). At RU and SW, water transport broke down in 2018 well before DOY 200. At LO, LA1 and LA2, the decline in late summer/autumn 2018 was much more gradually and, at LA1 and LA2, followed the pattern observed in 2017, in which year the mid-summer values were lower than in 2018, as was the mean VPD (Fig. S4). It should be noted that at RU no recovery of sap flow rates was observed in autumn 2018 after the rainfall, contrasting with the behavior at SW.

When plotting hourly sap flow rates vs VPD (Suppl. Fig. S5), we could estimate canopy conductances from the initial slope in the range below 1 kPa VPD (see Section 2.5; Table 1). In 2018, the highest values were observed in early summer at all sites, ranging from the 0.088 mm s<sup>-1</sup> at the sparse stand in LO to 0.746 mm s<sup>-1</sup> at LA1. At the height of the drought stress period, only (very) low increases of sap flow rates with increasing VPD – and thus canopy conductance – were recorded at RU, SW and LO, while at the LA sites a decrease to approximately one half of the June values was observed.

## 4. Discussion

### 4.1. Water supply and leaf shedding in summer 2018

While there was abundant soil moisture available in summer 2017 (Fig. S2) for an assumed bulk root depth for oaks of < 1 m (Thomas and Hartmann 1998, own observations on uprooted trees at RU and LA1), the extremely warm and dry summer 2018 led to a strong negative climatic water balance at all sites. Since the trees were unable to extract water from the upper soil layers, they became fully dependent on groundwater or capillary water access (sandy soils) or rock fissure water (LO) for most of July and August, even ranging into September, accessible only by a smaller fraction of deep roots of unknown length. Obviously, as reflected in the (gradually) different patterns of

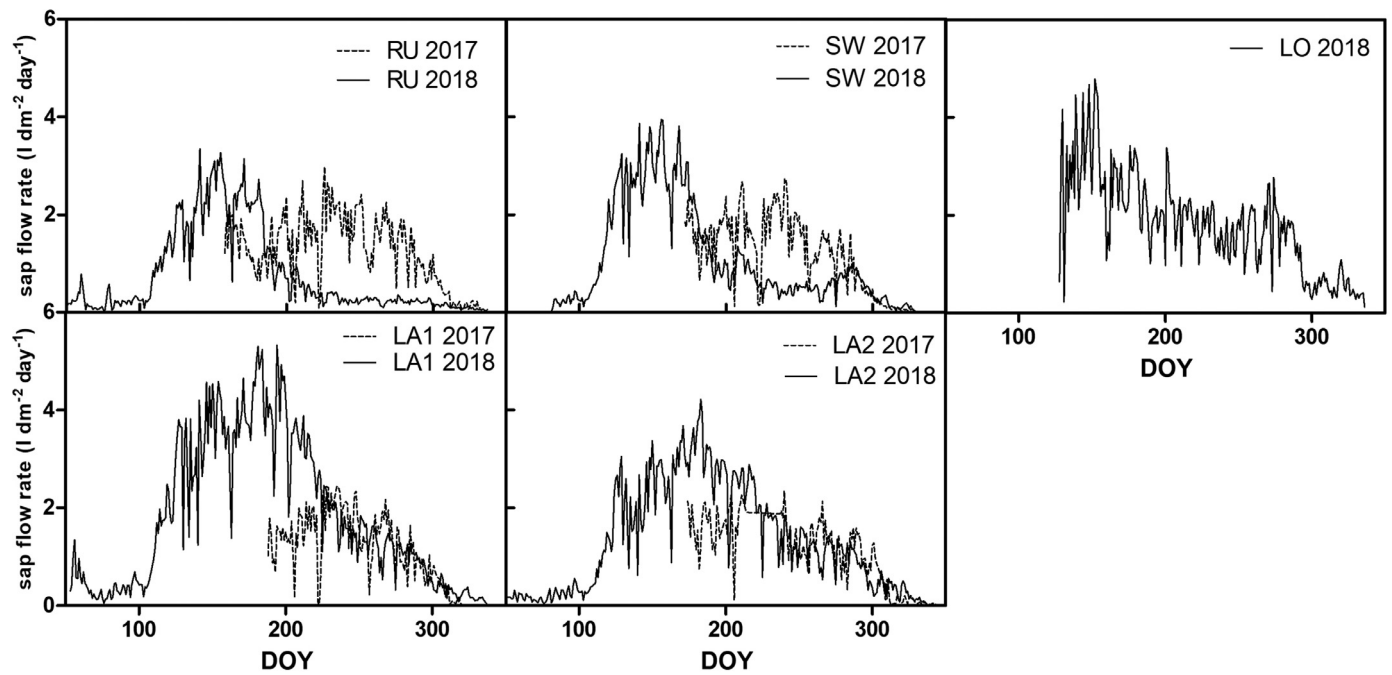


Fig. 3. Daily sap flow sums (means of usually 5 trees per site and date, for temporary recording failures of individual sensors cf. Table S2) during the vegetation period 2018 and, for comparison, the second half of 2017 (dotted lines).

sap flow rates and  $\Psi_{PD}$  at the different sites, water supply from the deeper soil layers must be different in the different sites (Figs. 2, 3), despite very similar ground water tables and precipitation patterns (Figs. S1, S2). Apparently, the limited water supply was insufficient to allow the trees to maintain their full crowns and leaf shedding occurred at all sites (Fig. 1), accompanied by chl content decreases in RU (20% in the course of July and proceeding through August). Partial summer defoliation in European broadleaf trees has been documented during the summer 2003 heatwave for beech and pubescent oaks (Granier et al., 2007; Zweifel et al., 2007). However, the relative amount of defoliation observed in our study was much larger than in the study reported by Granier et al. (2007) for beech, who reported a loss of approximately  $1 \text{ m}^2 \text{ m}^{-2}$  at a basic PAI (plant area index) value of 12 (including light interception by stems and branches, which were subtracted in our LAI values). Whether this defoliation should be considered as an inherent drought avoidance mechanism, as it is the case for deciduous tropical species during the dry season, appears questionable to us, since in the documented cases large amounts of the shed leaves were either rapidly “sunburnt”, i.e. turned from green to white from one day to another (Zweifel et al., 2007) or were still green (Bréda et al., 2006, this study), i.e. an orderly removing of nutrients, as during the deciduous process, could not take place. The mechanism of (irregular) leaf abscission in beech and oak by drought has not been clarified yet; Bréda et al. (1993) and Granier et al. (2007) suggest (irreversible) petiole xylem embolism as the driving factor.

#### 4.2. Tree water relations

The strong, but reversible decreases in  $\Psi_{PD}$  well below  $-2 \text{ MPa}$  and in RWC to 73–85% (Fig. 2) indicated severe water stress, the strongest stress being observed at RU ( $-4 \text{ MPa}$ ). Very low  $\Psi_{PD}$  values for adult, deciduous oaks at natural stands have been reported from the Mediterranean, e.g. for *Qu. pubescens* near Montpellier, France, in summer 1994 [ $-4.5 \text{ MPa}$ ; Damesin & Rambal (1995)], and also in summer 2003 in Switzerland for *Qu. pubescens* ( $-2.5 \text{ MPa}$ , Haldimann et al., 2008) and *Qu. petraea* ( $-1.5 \text{ MPa}$ , Leuzinger et al., 2005), but the extent to which  $\Psi_{PD}$  decreased at RU has, to our knowledge, not been reported yet from Central European forest stands of *Qu. robur* or *Qu. petraea*. In this con-

text, it should be remembered that although 3 out of the 5 measured trees at RU survived this extreme stress and recovered with respect to  $\Psi_{PD}$ , two were uprooted by the wind gusts of a thunderstorm in September. Thus, the extreme decrease in  $\Psi_{PD}$  itself was not lethal to the trees, but we conclude from theoretical considerations that the extreme drought also led to a significant weakening of the root system: The maxima of 22–23 m/s wind speed recorded during this event were below the values observed in earlier winter storms (25–28 m/s at Frankfurt airport during the storms “Kyrill” on 18.1.2007 and “Friederike” on 18.1.2018 (DWD)), which were devastating in Northwest Germany, but yielded only moderate damage in the forests of the middle Rhine and Main valleys and did not affect the stand at RU. Further, they are at the lower edge of wind speeds necessary to uproot even 30 m tall, fully leaved Douglas firs in exposed stands (Schelhaas et al., 2007). On Sep 26th, 2018, crown cover had already decreased from an LAI over 4 (in early summer) to just above 2, meaning that the approximately 11.5–14.5 m tall trees, inside the forest, cannot have been exposed to extreme leverage forces.

In the early leaf development phase in 2018 until approximately DOY 130,  $F_D$  increased simultaneously with leaf expansion until maximum values of  $0.4 \text{ L dm}^{-2} \text{ h}^{-1}$ , summing up to 3–5  $\text{L dm}^{-2} \text{ day}^{-1}$  (Fig. 3 and S5A) (cf. also Čermák et al., 1982; Bréda and Granier 1996). These values are somewhat lower than those measured under good water supply in Tuscany by Grossiord et al. (2014) for *Quercus petraea* on cambisol (maximum 0.6 to  $0.7 \text{ L dm}^{-2} \text{ h}^{-1}$ ). In contrast to the Grossiord et al. (2014) study and to the sites at LA and LO, where  $F_D$  later declined gradually to about half its maximum value in the course of the summer drought, they broke down quite dramatically at RU in June and at SW in July (Fig. 3). The drastic changes in  $F_D$  in RU and SW were reflected in a complete loss of responsiveness of the stomata to VPD from 0.135 to 0.165 (May, June) to below  $0.03 \text{ L dm}^{-2} \text{ h}^{-1} \text{ kPa}^{-1}$  (Fig. S5A, Table S3). At RU, despite the recovery of  $\Psi_{PD}$  in September after rainfall in branches accessible from the ground, no significant recovery of  $F_D$  was visible in autumn (cf. Fig. 3). However, when  $\Psi_{PD}$  decreases beyond  $-2.7 \text{ MPa}$ , irreversible xylem embolism can occur in *Qu. petraea* (Cochard et al., 1996). Since many trees also showed branch death above 3 m height (own observations in 2019), we conclude that significant em-

bolism had taken place during the drought period (cf. Bréda et al., 1993). The wind falling of many oaks in late September indicated that the prolonged drought may also have damaged large parts of the root system in this site. At SW, recovery of  $g_c$  occurred to half its early summer value, with leaf area also declining to less than a half during the drought period, meaning that the responsiveness of the stomata of the remaining leaves more or less retained their early summer values. In contrast to RU and SW, trees at LA maintained a moderate responsiveness of  $F_D$  to VPD under severe drought (Fig. S5B, Table S3).

Canopy conductance in general strongly depended on site and water availability and ranged at maximum to  $0.845 \text{ mm s}^{-1}$  (Table 1). Higher values have been reported by Hogg and Hurdle (1997) (around  $6 \text{ mm s}^{-1}$ ) for a mature aspen stand under good water supply, and Granier and Bréda (1996) arrived at maximum  $g_c$  values of  $10\text{--}15 \text{ mm s}^{-1}$  for a dense, 35-year-old *Qu. petraea* stand near Nancy, east France, on a loamy soil above gley with similar annual precipitation as in the Rhine-Main valleys. Loamy soil retains water much better than the sandy ground in our plots. Thus, the oaks in our (drought-prone) stands operate at best at approx. 5% of the canopy conductance observed near Nancy.  $g_c$  is calculated from the initial slope of the  $F_D$  vs VPD curve, thus from the  $F_D$  values reached at or near a VPD of 1 kPa, and from tree density in the stand and relative sap wood area. In the case of Granier and Bréda (1996), maximum  $F_D$  values observed were approximately 5-fold higher than in our study and in the Grossiord et al. (2016) report. In addition, relative sap wood area and stand density were much higher in the Granier and Bréda (1996) study, combining to approximately 3-fold the values observed in LA2, thus resulting in a 15-fold higher value of  $g_c$  than in our case. Oak tree architecture (i.e. shoot/root ratios, root system development, Grossoni et al., 1998, Bussotti et al., 2002), and leaf anatomy (Bruschi et al., 2003) can react very plastic to water supply. We conclude that the younger oaks in the Granier and Bréda (1996) study had not undergone strong intraspecific selection by drought yet, since the loamy soil at their stand will retain water much better than the sandy soil in our stands. In contrast, the trees in our study are the survivors of intra-population selection by frequent drought events, their crowns are adapted to much lower water availability and, in addition, they may have lost a larger proportion of xylem conductivity from previous years through irreversible embolism, thus explaining the low maximum  $F_D$  rates.

In vegetation modelling, a minimum value of  $0.5 \text{ mm/s}$  is used as the default value to describe the temperate summer-green deciduous European forest-type (Smith et al., 2001). This value is clearly undercut in the stands at SW, RU and LO, even under good water supply, indicating that the threshold values for  $g_c$  in vegetation modelling for the dry edge of oak forests in central Europe should be reconsidered.

#### 4.3. Site-specific effects of groundwater and capillary water

As long as sufficient rainfall occurs during summer, like in 2017, European deciduous oaks (*Qu. robur*, *Qu. petraea*, *Qu. pubescens*) can be supported by water in the upper 1–2 m soil layer (Bréda et al., 1993). In 2018, however, the upper soil completely dried out during summer (Fig S2), and for maintaining water uptake, sap flow and photosynthesis, trees would rely on direct access to groundwater, or access to capillary water and/or on hydraulic lift of deeper ( $> 1 \text{ m}$  depth) water, which has been reported for *Qu. petraea* (Zapater et al., 2010). This dependence on groundwater aquifers has been shown for the area of LA (and further southern stands in the Rhine valley) by the observation that groundwater extraction in the floodplain forests renders radial growth of *Qu. robur* more susceptible to drought years (Skiadaresis et al., 2019). If groundwater tables are several m deep (Fig. S1), direct groundwater access can be excluded and the factors determining water uptake in the absence of precipitation are the potential root length, which, in the case of *Qu. robur*, can be significantly longer in sandy soil ( $>180 \text{ cm}$ : Früchtenicht and Brüg) than in loamy soil (100–160 cm, Bréda et al., 1993, Arend et al., 2011, Früchtenicht et al. 2018) and the potential

maximum distance and rate of upward movement of capillary water from the groundwater table.

Since we were unable to directly measure water fluxes in the soil, the following considerations must be seen as a theoretical approach to understand the different water uptake behaviours of the trees in the LA sites and at SW and RU, on the other hand, despite similar, experimentally observed ground water levels: The potential distance of vertical capillary water transport in sandy soil has been studied, among others, by Grünberger et al. (2011), in Morocco during a drought season, with a ground water aquifer at approximately  $-2.5 \text{ m}$  depth. At  $1.5 \text{ m}$  above the groundwater level, volumetric water contents of 7–8% were observed, sufficient for plant water uptake, and solely supplied by capillary water movement. To sustain the measured sap flow rates in LA of approximately  $2 \text{ L dm}^{-2} \text{ day}^{-1}$  in August (Fig. 3), at a sapwood area of roughly  $0.05 \text{ dm}^2 \text{ m}^{-2}$ , and accounting for the empirical correction factor of 2 (cf. Section 2.5), we arrive at a necessary water supply of  $0.2 \text{ mm day}^{-1}$ . The rate of capillary water supply can be estimated according to Raes and Deproost (2003): roughly, in a sandy soil under Central European conditions, upward capillary transport can amount to approximately  $0.2 \text{ mm day}^{-1}$  from a  $1.5 \text{ m}$  deeper (groundwater) aquifer (and more from shallower aquifers). Thus, at LA a root length of  $2.5 \text{ m}$  would be sufficient to explain the observed sap flow rates by capillary transport from the groundwater table (ca.  $-4 \text{ m}$  in August 2018). A notable difference between LA1 and LA2 was the much higher LAI at LA2, due to the closed canopy vs the open, drought and storm-damaged stand at LA1. Concerning the estimated canopy conductance, however, this was compensated by a higher  $F_D$  at LA1 than at LA2 and both sites revealed quite similar estimated  $g_c$  values. Although  $g_c$  is underestimated in LA2 because of an overestimation of  $\Delta\text{VPD}$  due to the denser canopy, we interpret this finding as an indicator that rather water supply and not leaf area limited trunk water transport, in accordance with Granier et al. (2000), who suggested that beyond a LAI of approximately 5–6,  $g_c$  goes into saturation even under good water supply.

Evidently, at RU and SW the trees lost their connection to soil water in the course of the summer (Fig. 3). At SW, this occurred at critical ground water tables around  $-4.1 \text{ m}$ , well into the gravel / sand layer below the top sand layers. Due to the coarse texture of the soil material here, capillary forces to move groundwater upwards must be much weaker than in the study by Grünberger et al. (2011) and cannot transport water as high as ( $-4.1 + 1.5 =$ )  $-2.6 \text{ m}$ . We therefore suggest that the trees at SW had no access to ground or capillary water during late summer 2018. At RU, a coarse texture of scree / sand was observed below a sand layer of  $3.75 \text{ m}$  (below clay) in the vicinity ( $350 \text{ m}$  southwest) of the stand site. Therefore, we tentatively assume a similar situation here as in SW, with the groundwater table retracting into a much coarser layer, leaving insufficient capillary water transport for the trees. It should be noted, that during the subsequent equally dry summers 2019 and 2020, significant dieback in *Qu. robur* stands occurred with up to 80% losses (own observations), both at RU and also at SW, indicating that the species, which has inhabited the sandy terraces of the Rhine-Main valleys for (at least) many hundreds of years, now already reaches its distribution boundary here under continued drought years, as expected from vegetation modelling for future climate change scenarios (e.g. Hanewinkel et al., 2013). This scenario is supported by the Annual Reports on forest status published for the whole province of Hesse (Table 2). The site at LO differs from the sites in the fluvial sand-dominated Rhine and Main valleys by its shallow soil on a steep schist slope. Here, trees were able to maintain (constantly decreasing) water transport throughout July and August at similar sap flow rates as in LA (Fig. 3). Their estimated maximum canopy conductance, however, was much lower than at LA (Table 1), due to the low SA and the closed stomata, visible in the complete loss of responsiveness in the  $F_D$  vs VPD curves between DOY 148–224 (Fig. S5B). Hence, the trees at LO resembled the behaviour of *Qu. petraea* on a calcareous slope near Basel Switzerland, in the extreme summer of 2003 (Leuzinger et al., 2005), which also maintained significant sap flow rates during long-term drought, in contrast to

**Table 2**

Summarized data on the status of oaks (*Qu. robur* and *Qu. petraea* in the state of Hesse 2016–2019 (compiled from HMU(K)LV 2017, 2018, 2019, 2020).

		2016	2017	2018	2019
T vegetation period	Deviation from 1961 to 90 average	1.7	1.2	3.0	1.2
Prec. vegetation period	1961–90 average: 350 mm	300	440	200	300
Crown damage	% of trees	32	32	36	46
Fructification	% of trees	17	24	43	n.d.
Insect pest damage	% of trees	1.5	12.0	2.0	3.0
Mortality	% of trees	1.5	<<1.0	1.0	0.9

beech trees at the same site. The authors concluded that the oaks were able to maintain water uptake by access to residual water in deeper rock fissures and that beech - even if it were also able to reach these water resources, suffered from xylem embolism, which inhibited sap flow rates. Recovery of leaf water potential at LO was not complete in *Qu. petraea* after the September rain (Fig. 2), indicating that water availability differed from the situation in the valley stands, because a large proportion of the heavy rain on Sep 23rd left the system as runoff water.

## 5. Conclusions

i) The extremely hot and dry summer 2018 had a severe, but differential impact on oak (*Quercus robur*, *Qu. petraea*) crown cover and water relations in stands along the Middle Rhine and lower Main valleys, four with sandy soil and one schist slope, all situated in the same mesoclimate, but representing an ecological gradient from moderate to severe drought. ii) As long as a combination of ground and capillary or rock fissure water supplied mature oak trees, trees were able to cope with the extreme heat / drought situation by partial early leaf shedding. However, in two sandy stands, at SW and at RU, water supply was insufficient to maintain even moderate sap flow rates. We suggest that this was due to a retreat of the groundwater table to deeper soil layers with coarse texture (pebble, scree), thus preventing capillary water transport to the root systems. iii) Estimated canopy conductance varied significantly in the course of summer 2018 and between sites, depending on drought duration and (deep) soil conditions. It strongly depended on ground water / capillary water access during the driest period and, of course, on stand density, which was adapted to the local potential water supply by intra-population selection during the growth of the stand. In the strongest affected sites, drought-induced leaf shedding (at SW and RU) and probably, xylem embolism and root system damage (at RU) prevented canopy conductance to return to pre-drought values after autumn rainfall.

## Declaration of Competing Interest

The authors declare no conflict of interest.

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## Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.stress.2021.100010.

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