Transpiration and water potential of young *Quercus petraea* (M.) Liebl. coppice sprouts and seedlings during favourable and drought conditions

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Abstract

Stojanović M., Szatniewska J., Kyselová I., Pokorný R., Čater M. (2017): Transpiration and water potential of young *Quercus petraea* (M.) Liebl. coppice sprouts and seedlings during favourable and drought conditions. J. For. Sci., 63: 313–323.

Increased frequency and intensity of drought events consequently affect oak high forests with the process of further decline, compromised growth and questionable natural regeneration. To overcome such difficulties, new adaptive strategies are required. Coppicing, as the oldest way of forest management, might provide some solutions. In our study two contrasting management systems, sessile oak coppice and high forest, were compared at the initial stages of regeneration and forest development. The transpiration of young oak sprouts and seedlings was monitored using sap flow systems during the 2015 growing season. The study of transpiration also included leaf water potential measurements during three measurement campaigns with contrasting weather conditions.
Coppice sprouts transpired significantly more than seedlings on the individual tree and stand level during the entire growing season 2015; particularly large differences were observed during drought conditions. Coppice sprouts experienced lower water limitations due to the voluminous and deeper root system as indicated by leaf water potential results. Presented results attribute young coppices as one of the promising adaptable forest management types with a better adaptive strategy at the extreme sites under water limiting conditions.

Keywords: sessile oak; management system; comparison; sap flow; leaf water potential; water availability

Drought affects growth, disturbs water relations and water use efficiency of plants (Pietras et al. 2016), alters nutrient uptake and reduces photosynthesis (Stojanović et al. 2016) and may lead to hydraulic failure and carbon starvation (McDowell 2011). It increases the susceptibility to abiotic and biotic stress factors (McDowell 2011; Ryan 2011). The global climate change models presume a more frequent occurrence and higher severity of droughts in the future (IPCC 2007). Owing to those predicted climate changes, proper silvicultural treatments are required (Kohler et al. 2010).

Coppicing is one of the oldest silvicultural systems (Matthews 1991; Fujimori 2001) that has been practiced over large spatial scales in Europe, providing a regular supply of firewood and it has

significantly shaped the present structure and composition of forest ecosystems (Rackham 2008). The system is based on new resprouting from both the stumps and roots of deciduous broadleaved trees, if cut down periodically (Del Tredici 2001). Matula et al. (2012) described sessile oak (*Quercus petraea* /von Mattuschka/ Lieblein), hornbeam (*Carpinus betulus* Linnaeus) and lime (*Tilia* spp.) as the main tree species of central European coppices. During the mid-20th century coppice forests were either converted into high forests or abandoned (Altman et al. 2013). The coppice abandonment caused a reduction of the herbaceous plant species and endangered invertebrates, and also negatively influenced some tree species, particularly light-demanding and pioneer ones (Kopecký et al. 2013). Recent interests in restoring coppices in Europe were mostly driven due to their positive influence on biodiversity and protecting endangered species (Kopecký et al. 2013; Vild et al. 2013). Several studies have proven the beneficial effect of re-introducing traditional management in abandoned coppices (Kopecký et al. 2013; Vild et al. 2013). Nevertheless, the opening of abandoned coppices creates conditions (increased light and soil temperature) for higher nitrogen mineralization and thus it may pose threats to biodiversity by enhancing the spread of nitrogen-demanding ruderal species (Vild et al. 2013).

Today, oak high forests in Europe are naturally regenerated using shelterwood systems, where a mature stand is gradually removed during the period of 10–20 years (Attocchi 2015). Seeding and planting are used when the acorn production is not sufficient for regeneration, especially in the last decades due to unfavourable water conditions and extreme weather events (Annighöfer et al. 2015; Attocchi 2015).

The main concerns regarding oaks are connected with successful advantageous regeneration (Annighöfer et al. 2015), as oak forests are losing their ability to successfully regenerate (Altman et al. 2013) due to various reasons (browsing, uneven age classes, former management, change of the site conditions and extreme weather events). Abandoned oak coppices and consequently low cutting intensities favour shade-tolerant species which may prevent oaks to reach the mature phase and produce acorns (von Lüpke 1998; Dobrowolska 2006). According to Altman et al. (2013) successful regeneration of oaks in coppices was probably conditioned by the frequent recurrence of light pulses which may have provided the long-term survival of the species.

Recently, a trend of replacing the coniferous species with the broadleaved species (Bednář, Černý 2014), especially oak and beech, which are the two most economically important broadleaved species in the Czech Republic (Ministry of Agriculture of the Czech Republic 2012), has been established (Klimo et al. 2000). The former focus of larger forest owners has been targeting mostly Norway spruce (*Picea abies* (Linnaeus) H. Karsten) and Scots pine (*Pinus sylvestris* Linnaeus), as a consequence of the former German forestry school from the beginning of the 20th century and promotion of conifers due to sufficient increment, production characteristics, and favourable merchantability, even on some inappropriate sites (Klimo et al. 2000; Dobrowolska 2006). Nowadays, oak forests cover more than 170,000 ha (7.4% of total forest area) in the Czech Republic (NFI 2007). According to Březina and Dobrovolný (2011) the long-term silvicultural target of Czech foresters is to increase the proportion of oaks in the Czech Republic's lowlands as it is known that oaks are well adapted to the predicted warmer and drier conditions in Central Europe (Bolte et al. 2009). It is also likely that the ecological and economic role of oaks would increase in Central European forests and forest management (Rigling et al. 2013; Schelhaas et al. 2015). Nevertheless, oak forests have experienced a decline during the last three decades, caused by various effects (Führer 1998; Thomas et al. 2002). The phenomenon is often referred to as "oak decline" in the literature. Studies agree that the reason for oak decline is the combination of several factors such as winter frost, summer drought, ageing, anthropogenic worsening of the site, insect defoliation and infection by pathogenic fungi.

Two contrasting silvicultural systems – high forest (generative origin; seedlings) and coppice forest (vegetative origin; sprouts) – affect tree water use, especially during droughts. Different regeneration types provide different dispositions for the establishment of regeneration. According to Hochbichler (1993), the main strength of coppices in drought affected areas is the absence of unfavourable germination and juvenile phases, present under generative regeneration. Coppice sprouts use the well-developed root system of a previously established tree, while seedlings need to develop their own belowground structures (Bond, Midgley 2001). As seedlings initially demonstrate a reduced ability of resource uptake from the soil, they might be more susceptible to water and nutrient stress (Savé et al. 1999).

In the present study, the water status of young sessile oaks growing in high and coppice forests was compared. We also analysed plant transpiration, leaf water potential in relation to the applied silvicultural system and microclimatic conditions, particularly during drought conditions. The study aim was to examine how tree origin and applied silvicultural method determine the plant water status, particularly during drought stress conditions.

MATERIAL AND METHODS

Study area. The study area is located in the South Moravian region in the southeast of the Czech Republic (Fig. 1) in a mixed *Carpineto-Quercetum* forest (PLÍVA 1987). The study was carried out in two forest stands (3.2 km apart) dominated by sessile oak that have experienced the two past management practices. Both sites were acid and rocky, mainly illimerized soils on loamy alluvium and granodiorite with an inaccessible groundwater table, drying out in summer (PLÍVA 1987).

The average (1951–2015) air temperature was 7.5°C and the total annual sum of precipitation varied from 550 to 650 mm. The region is considered as one of the driest in the Czech Republic (BRÁZDIL et al. 2013). A young high stand was established by the shelterwood method on 3.9 ha of the sessile oak high forest (BŘEZINA, DOBROVOLNÝ 2011). A coppice forest was established by clear cutting of a 95-year-old coppice (4 ha) stand with a 95% share
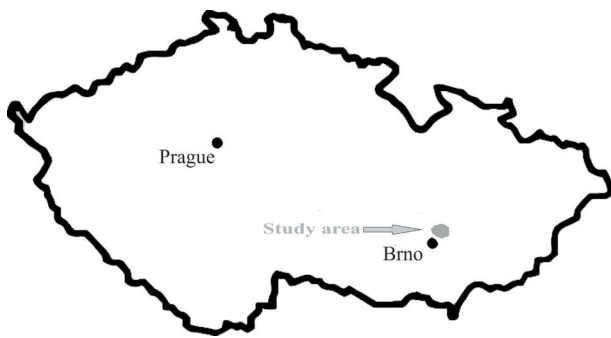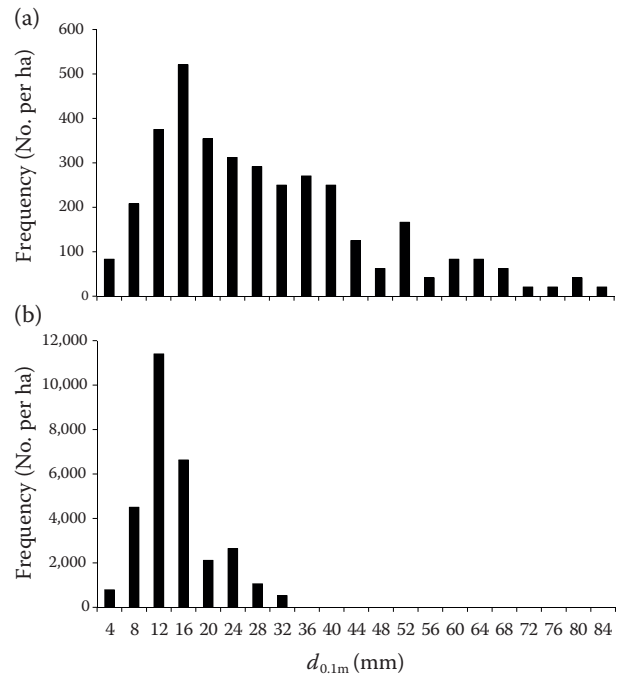
Fig. 2. Stem diameter structure of the studied coppice – Soběšice (a), high forest – Vranov (b) stand

$d_{0.1m}$ – stem diameter of coppice sprouts and seedlings at 0.1 m above the stump or ground

of sessile oak (KADAVÝ et al. 2011).Young high and coppice stands were of comparable age (5–6 years). The age of both seedlings and sprouts was estimated by a destructive method at the end of 2015.

Structural analysis showed that coppice and high forest at a regeneration stage differ significantly in tree distribution and in stem diameter classes (Fig. 2). Also, trees had different spatial distributions. In coppice, trees were clumped around stumps, while in high forest trees were distributed more evenly, as a consequence of the applied management method. The mean stem diameter and mean tree height were significantly higher in coppice than in high forest (Table 1). Oppositely, stand density was eight times higher, and leaf area index almost twice higher in the high forest, compared to the coppice stand (Table 1).

Sap flow and transpiration. To estimate water consumption in two management systems, sap flow sensors were installed on eight seedlings and

Fig. 1. Location of the study area

Table 1. Structural characteristics of the oak regeneration in the studied coppice and high forest stands

	Coppice	High forest
Mean stem diameter at 0.1 m ± SD (mm)	27.37 ± 17.51	12.55 ± 8.42
Mean tree height ± SD (cm)	231.28 ± 82.09	114.03 ± 49.49
Basal area (m²·ha⁻¹)	3.02	4.28
Stand density (in thousands per hectare)	3.6	20.7
Leaf area index (m²·m⁻²)	0.51	0.98

SD – standard deviation

eight sprouts at both sites. Sap flow measurements were conducted from May until mid-October, comprising a period of 157 days in 2015. The sap flow instruments were installed below the foliage at heights from 25 to 45 cm above the ground/stump at points where the stems were straight, their surfaces smooth, free of knots and their diameters ranged from 12.2 to 20.0 mm and/or from 10.8 to 17.7 mm for sprouts and seedlings, respectively (Table 2). Sap flow measurements were used to calculate mean hourly and daily whole plant water fluxes.

Sap flow was measured using commercially available EMS 62-type measuring sensors (EMS Brno, Czech Republic). The measuring principle is based on the stem heat balance method with external heating and internal temperature sensing (Lindroth et al. 1995; Pietras et al. 2016).

The system uses heat provided by a resistance wire, and heat balance of the artificially heated part of the stem, as described in Eq. 1:

$$P = Q \times dT \times c_w + dT \times c_w \qquad (1)$$

where:

P – input heat power (W),
Q – sap flow rate (kg·s^{-1}, cm),
dT – temperature difference at the measuring point,
c_w – specific heat of water (J·kg^{-1}·K^{-1}).

Subsequently the sap flow rate is calculated by Eq. 2:

$$Q = \frac{P}{c_w \times dT} - \frac{\lambda}{c_w} \qquad (2)$$

where:

λ – coefficient of heat losses from the measuring point (W·K^{-1}).

The temperature difference between the heated and unheated parts of the measuring point (4K) was kept constant and measured by thermocouples inserted approximately 2–3 mm into the xylem. The input power needed to maintain the fixed temperature difference was proportional to the amount of water passing the sensor. Thermal insulation was provided by accompanying foam and radiation shields. Measurements were conducted every minute, while data averages were recorded at ten-minute intervals. The heat losses from the sensors were eliminated from the total sap flow value on the basis of baseline subtraction at 03.00 a.m., when actual sap flow was assumed to be zero, by daily baseline subtraction in Mini32 (Version 4.4.16.0, 2016).

A period with non-limiting soil water conditions (soil water potential > −0.5 MPa) was chosen from

Table 2. Height (h), diameter ($d_{0.1m}$), diameter at sensor height (d_s), specific leaf area (SLA) and leaf area (LA) of the seedlings and/or coppice sprouts at the end of the experiment used for sap-flow measurements

Sensor No.	d_s (mm)	$d_{0.1m}$ (mm)	h (cm)	SLA (cm^2·g^{-1})	LA (m^2)
Sprouts					
1	19.6	24.7	215	133.08	1.65
2	20.0	32.7	330	132.39	1.90
3	19.0	26.1	279	127.56	1.75
4	12.2	16.8	306	122.06	0.83
5	12.6	15.2	140	139.73	0.67
6	11.7	12.3	138	128.19	0.49
7	12.3	14.5	119	120.76	0.48
8	18.6	28.0	248	133.76	1.49
Seedlings					
1	16.3	23.8	206	137.31	1.04
2	15.0	21.1	176	167.16	1.09
3	17.7	19.7	179	163.60	1.00
4	16.1	20.3	227	143.19	0.98
5	10.8	13.4	107	154.46	0.30
6	10.9	14.3	174	160.87	0.53
7	11.2	14.0	156	155.67	0.34
8	11.4	16.5	156	167.42	0.59

the entire period of sap flow measurements and used for analysis between mean daily sap flow and dendrometric parameters of the plant. According to the coefficient of determination of regression analyses, the best scaling factor was chosen. Sap flow was significantly related to plant leaf area (LA) and stem diameter at 0.1 m above the stump/ground – $d_{0.1m}$ (mm). Sap flow scaled to plant LA was expressed as seedling and sprout transpiration – Q (kg·m^{-2}·h^{-1}). This allowed a proper comparison of the coppice sprouts and seedlings as the size of the plants had no influence on water consumption. Likewise, sap flow scaled to plant $d_{0.1m}$ was used to upscale sap flow values from sample trees to the entire stands – E (mm·day^{-1}).

For the leaf trait study, approximately 16 leaves per coppice sprout/seedling (10 individuals per stand) were taken randomly from the upper third of the tree-crown height, three times during the growing season (480 leaves per stand). Fresh leaves were scanned and the average projected leaf area was calculated using ACC program (Version 5.0, 2002). Afterwards, leaves were dried at 105°C to constant weight, and weighed to the nearest 0.001 g. The specific leaf area – SLA (cm^2·g^{-1}), represented as projected fresh leaf surface area per leaf dry matter (Lambers et al. 2008), was calculated (Table 2). After the long-term sap flow measurements were completed in October 2015, the sampled

plants were harvested for the leaf area estimation and age structure. Before harvesting, biometric characteristics, such as plant height – h (cm) and $d_{0.1m}$ were assessed. Whole coppice sprout and/or seedling leaf material was collected and dried, as described above, to assess the total leaf dry mass of each individual plant. Subsequently, SLA and total leaf dry mass were used to assess the total projected plant LA (m^2 per sprout/seedling) (Table 2).

Diurnal leaf water potential. Water potential in leaves was measured according to Scholander et al. (1965) using a pressure chamber (PMS, Inc., USA). In order to establish diurnal courses of leaf water potential, measurements were carried out 7–8 times per day at 2-hour intervals from 04.00 a.m. until 07.00 p.m. on the 20th June, 22nd July and 15th September. Measurements were conducted on ten sprouts and ten seedlings every time. To avoid differences caused by illumination, leaves were collected both from the shaded and sunlit parts of the crowns. Three days were chosen as representatives of early-, mid- and late-summer conditions. Soil water potential and evaporative demands were different during these days. Stress factors were increasing through the summer due to rainfall shortage and high air temperatures culminating in the mid-summer period.

Microclimatic conditions. Microclimatic conditions were measured during the entire 2015 growing season (from March until November) in an open area above the grass surface, in the vicinity of both stands. Global radiation – GR (W·m^{-2}), air temperature (°C) and air humidity (%) at a height of 2 m above ground were measured by Minikin RTHi (EMS Brno, Czech Republic) at 1-min intervals. Precipitation (mm) was measured by MetOne 380 (EMS Brno, Czech Republic). All data were av-

eraged every 15 min and stored in the data logger memory. These microclimatic data were used to calculate vapour pressure deficit – VPD (MPa) and potential evapotranspiration – PET (mm) according to the FAO modified Penman-Monteith equation (Allen et al. 1998). Soil water potential – SWP (MPa) was measured by three gypsum blocks GB 2 (EMS Brno, Czech Republic) on each of the experimental sites. Gypsum block sensors were buried at a depth of 30 cm. Data were collected every hour.

Data analysis. Statistical analyses were done using the R statistical software (Version 3.3.2, 2016) and SigmaPlot® (Version 11.0, 2008). The Q and E of seedlings and sprouts and soil water and climatic conditions between stands were compared using the nonparametric Mann-Whitney-Wilcoxon test. Soil water potential data between stands were analysed by the t-test. To compare relations between sap flow, seedling/sprout biometry, simple and multiple regressions were used. Significance level was $P < 0.05$.

RESULTS

Sap flow and transpiration

Sap flow was well explained by a linear function depending on $d_{0.1m}$ (Fig. 3a), both for sprouts (R^2 = 0.95, $P < 0.0001$) and seedlings (R^2 = 0.91, $P = 0.0002$).

The relation between plant sap flow and bearing leaf area was explained by a power function and was used to compare the water use of sample trees (Fig. 3b). This relation was almost the same in coppice sprouts and high forest seedlings (R^2 = 0.98, $P < 0.0001$).
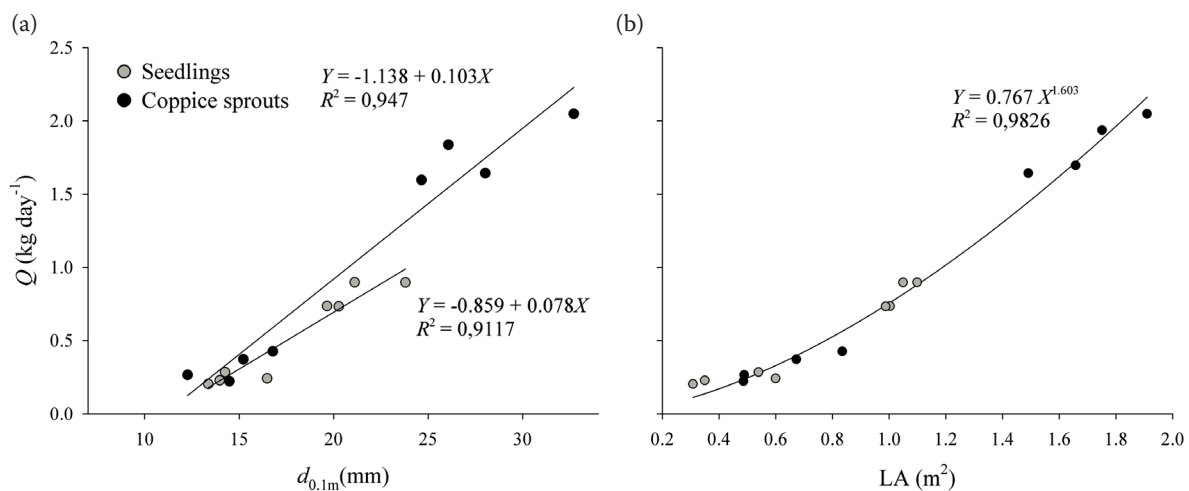

Fig. 3. Relation between the sap flow (Q) of sessile oak seedlings and sprouts and stem diameter at 0.1 m above the ground or stump – $d_{0.1m}$ (a), leaf area – LA (b)
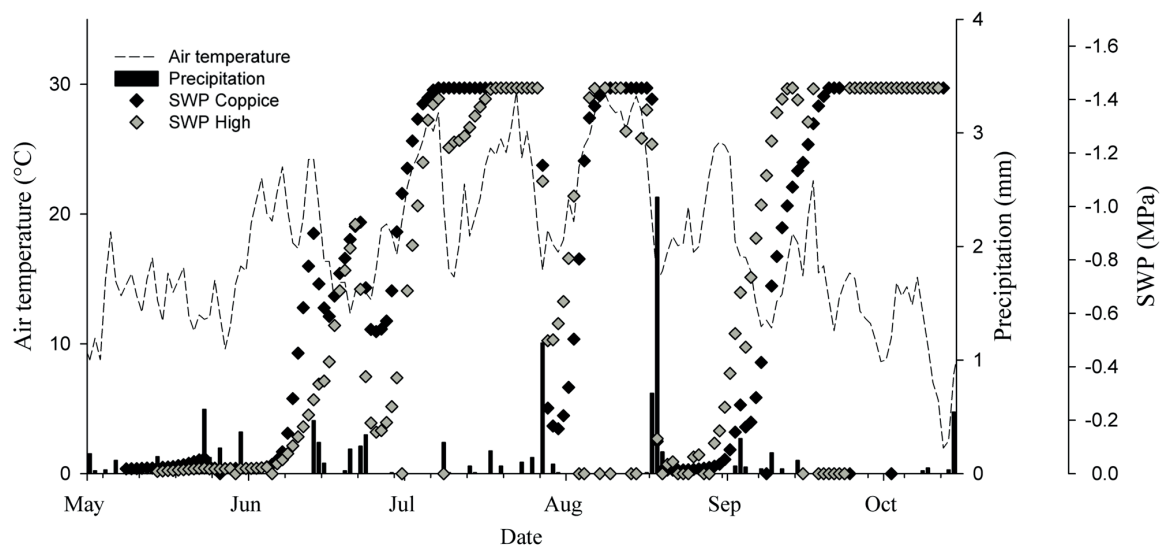
Fig. 4. Microclimatic conditions during the 2015 measurement period. Air temperature, daily values of precipitation and soil water potential (SWP) of the uppermost 30 cm of soil were measured during the experimental period. Mean values of SWP are presented separately for coppice stand and high stand

The sprouts and seedlings were experiencing similar soil water conditions on both experimental sites as no statistically significant differences were observed between soil water potentials (Fig. 4) in coppice and high stands during the entire measuring period (P = 0.892).

Sap flow, normalized by the plant leaf area, was significantly higher in coppice forest during the entire growing season, as the mean daily values of Q [± standard error (SE)] were 0.55 ± 0.04 and 0.17 ± 0.02 kg·m^{-2}·day^{-1} for sprouts and for seedlings, respectively (Fig. 5a). Likewise, the whole regenerated stand transpiration of coppice was much higher than that of high stand with the mean daily values of E (± SE) amounting to 0.41 ± 0.02 and 0.24 ± 0.02 mm·day^{-1}, respectively (Fig. 5b).

The differences in transpiration between the investigated systems were even more evident during drought periods (Figs 5a and 6). The plants were considered severely limited when SWP reached values of −1.4 MPa (HSIAO 1973) coupled together with high evaporative demands of the atmosphere and severe lack of rainfall (Fig. 4). Two 4-day periods with different atmospheric evaporative demands and soil water conditions were chosen for detailed evaluation of coppice sprout and seedling water consumption (Fig. 6).

As expected, differences in diurnal patterns on different days were observed and depended mainly on microclimatic conditions. During the drought period, the Q (± SE) reached 0.37 ± 0.04 in the coppice sprouts whereas only 0.07 ± 0.009 kg·m^{-2}·day^{-1} in the seedlings, which amounted to one half and one fourth of the values during favourable condi-
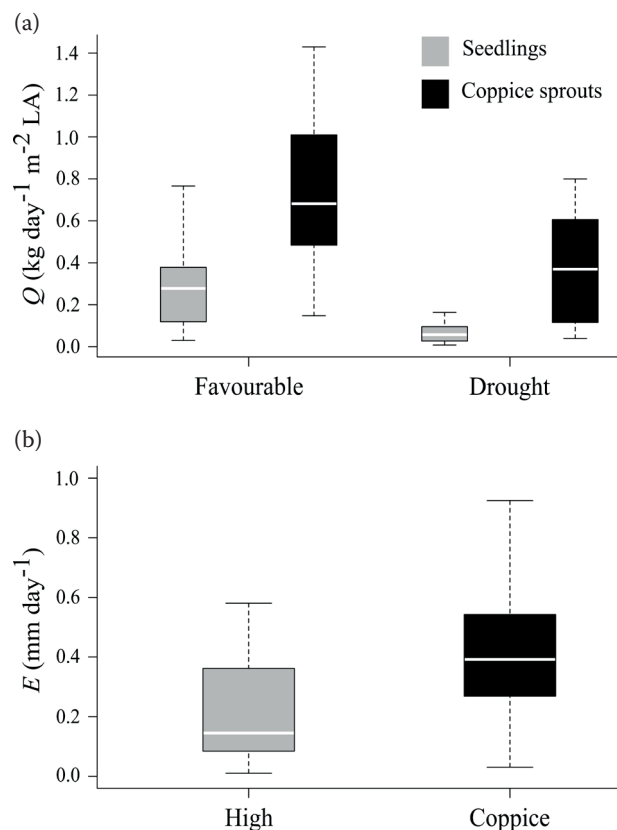

Fig. 5. High forest and coppice transpiration during the entire measurement period. The mean transpiration rate of coppice sprouts and seedlings during normal conditions [soil water potential (SWP) > −1.4 MPa] and during drought (SWP < −1.4 MPa) (a), stand transpiration for both stands during the entire measurement period (b) was measured

Q – sap flow scaled to plant leaf area (LA) and expressed as seedling and sprout transpiration, E – sap flow scaled to plant stem diameter at 0.1 m above the stump/ground to upscale sap flow values from sample trees to the entire stands
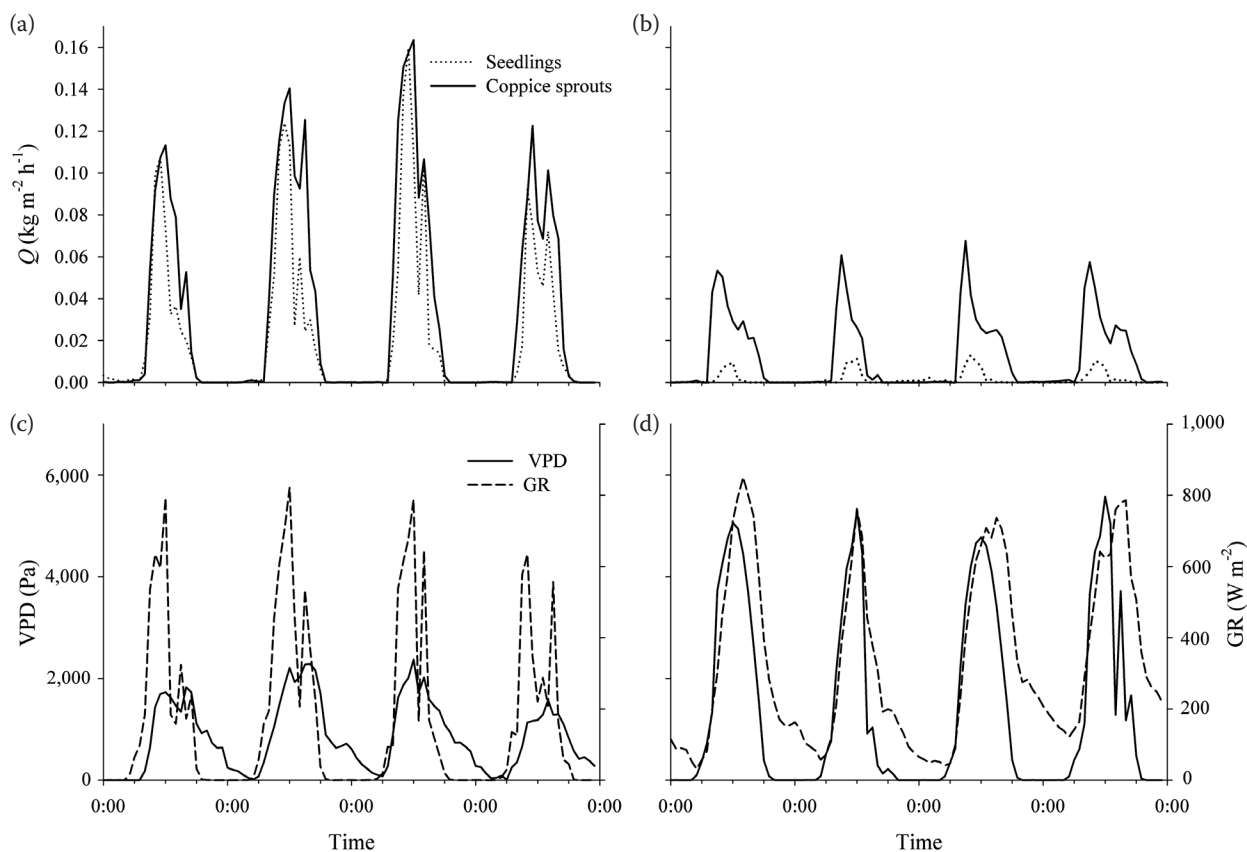
Fig. 6. The transpiration rate scaled to the leaf area of seedlings and coppice sprouts (*Q*) in relation to microclimate under favourable (a) and drought conditions (b); vapour pressure deficit – VPD (c) and global radiation – GR (d) under microclimatic conditions

tions (SWP > –1.4), respectively. Even when the soil water potential dropped below –1.4 MPa, the coppice forest showed a positive trend of transpiration and could meet evapotranspiration demands (Fig. 6). In contrast, seedlings in the high forest were not able to meet the increasing evaporative demand of surrounding air when soil water was limited.

Diurnal courses of leaf water potentials

To get the whole picture of the water status of two plant types sap flow studies were supplemented with leaf water potential. Throughout the experiment clear differences in the diurnal pattern of leaf water potential in relation to microclimatic conditions were observed. Three days chosen for campaign measurement differed in climatic conditions (Fig. 7): June 30 was characterized as warm but not dry (PET = 6.5 mm·day^{-1}, mean SWP = –1.1 MPa), July 22 as hot and dry (PET = 13.3 mm·day^{-1}, SWP < –1.4 MPa), and September 15 as cool and wet (PET = 0.8 mm·day^{-1}, SWP = 0.98 MPa).

The difference in leaf water potential between coppice sprouts and seedlings in non-limiting water conditions was not statistically significant, although less negative values in coppice sprouts compared to seedlings were observed during midday (Figs 7a, c). However, in July during severe drought conditions, the leaf water potential values in seedlings declined to about –3.5 MPa and varied little throughout the day, values in coppice sprouts were not dropping less than –2.8 MPa. The leaf water potential of seedlings and coppice sprouts differed significantly on "dry" days (*P* = 0.010), which indicates higher vulnerability of seedlings to drought (Fig. 7b).

DISCUSSION

On the basis of collected climatic data, such as rainfall patterns and SWP, we were able to recognize drought periods (Fig. 4). Severe drought was identified as periods of low (i.e. below-average) rainfall, with a relatively high temperature and VPD, and SWP dropping below –1.4 MPa (Hsiao 1973). The 2015 summer drought which hit Central Europe was the second driest (after 2003) in the last 50 years (Van Lanen et al. 2016). Maximum air temperatures for the Czech Republic during the growing season (April–September) and summer months
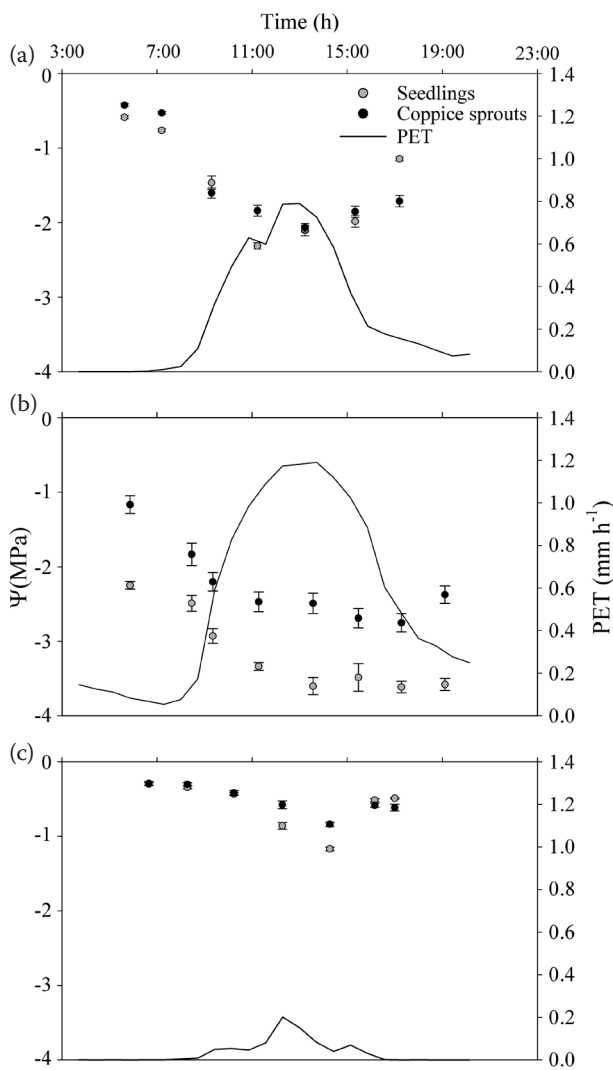
Fig. 7. Diurnal courses of leaf water potentials (ψ) in crowns of seedlings and coppice sprouts in relation to potential evapotranspiration (PET): June 30, 2015 (a), July 22, 2015 (b), September 15, 2015 (c). Error bars denote standard error of the mean

(June–August) were about 1.1 and 2°C higher than these for recent long-term averages (1981–2010), respectively (CHMI 2015). The area experienced a severe lack of rainfall and abnormally high evapotranspiration during the entire vegetation season (CHMI 2015). This was shortly alleviated by the abundant rainfall in mid-August (Fig. 4). However, it helped vegetation to slightly recover, this was not enough to end the overall drought situation, as the drought continued through September and October (CHMI 2015, Fig. 4). According to our microclimatic measurements, days under severe drought (SWP < –1.4 MPa) and moderate drought (–1.2 MPa < SWP ≤ –1.4 MPa) accounted for more than 35 and 40% of the whole measurement period, respectively (Fig. 4).

Drought has been suggested as the main cause of plant mortality (McDowell 2011; Ryan 2011;

Čater 2015). One of the main future challenges for the plants would be adaptation to changes in their environment as it will be crucial for their survival (Merchant 2016). Our study showed that sessile oak coppice sprouts are advantageous over seedlings, as they showed the better water status during the entire measurement period, regardless of weather conditions (Figs 5 and 6). Sprouts and seedlings largely differ in root systems (Bond, Midgley 2001). Coppice sprouts have a fully functional root system of a previously established tree (Bond, Midgley 2001) which ensures them more stable water resources (Vilagrosa et al. 2014). Therefore, coppice sprouts are minimizing the effect of water oscillations during the season by reaching the deeper soil layers (Vilagrosa et al. 2014; Pietras et al. 2016). Shallow roots and small root absorptive area were suggested as main reasons for lower transpiration rates of seedlings compared to sprouts (Pietras et al. 2016). Since seedlings rely on water in shallow soil layers where soil moisture availability is depleted rapidly (Gaines et al. 2016), this may justify the lower transpiration rates of seedlings as compared to sprouts. Nonetheless, the midday leaf water potential of seedlings was always found lower (more negative) than in coppice, these differences were pronounced mostly during drought conditions (Fig. 7). This confirms sufficient water availability to coppice sprouts, as it is known that tree species with deep root systems have a higher (less negative) pre-dawn water potential (Abrams 1990) due to an increase of soil water availability with depth and faster water refilling (Gaines et al. 2016). Drake et al. (2012) compared transpiration rates in *Eucalyptus globulus* Labillardière coppice and in its high forms, and they found higher rates of transpiration in coppice at a stand as well as individual tree level. Their findings were explained by the significantly higher leaf area index in coppice stand compared with high stand. However, in our case the high regenerated stand had the approximately 56% higher leaf area index than coppice, due to the higher number of individuals per hectare (Table 1), yet the high stand transpired less (Fig. 5). Likewise, it should also be taken into account that the year 2015 was extreme in terms of drought (CHMI 2015; Van Lanen et al. 2016), suggesting different water status and different stomatal control of both sprouts and seedlings when the soil water is limited.

In our study the leaves of coppice sprouts showed different adaptability from seedlings. According to many authors, leaves are adapted to the habi-

tat conditions but primarily to light regime and water conditions (Abrams 1990; Dickson, Tomlinson 1996). Lambers et al. (2008) stated that plants which adapted themselves to the shade conditions form thin leaves with a larger surface area, containing higher concentration of chlorophyll and water content in their tissues compared to sun adapted leaves/plants. On the other hand, leaves that are exposed to a larger quantity of light are characterised by lower surface area, formation of a few layers of palisade parenchyma, mesophyll, thicker epidermis and cuticle, higher dry mass with high-energy potential etc. SLA of sprouts was significantly lower than that of seedlings (*P* < 0.001, Table 2); this indicates a high amount of accumulated assimilates, thus the leaves of coppice sprouts were more sun-adapted and photosynthetically active. This was probably influenced also by the coppice structure, as sprouts are clumped around the stump, self-shading is smaller, therefore sprouts receive more direct sun irradiance from the open sides, whereas seedlings were densely stocked and were less insulated. Hence, a higher need for active evaporative cooling might be another reason for higher transpiration in young sprouts than in seedlings. Nonetheless, water availability may also influence the adaptation of leaves, hence the species adapted to a drier conditions tend to show lower values of SLA (Poorter et al. 2009). Reduction of SLA is assumed to be a way for plants to increase water use efficiency (Wellstein et al. 2017), which is contradictory to our results and expected lower values of seedling SLA as compared to coppice sprouts (Drake et al. 2012). However, the detailed physiological regulation of the SLA is still unclear (Poorter et al. 2009).

Oak species are adapted to drought-prone areas either by tolerating or avoiding drought stress (Abrams 1990; Dickson, Tomlinson 1996). Sessile oak seedlings at initial stages of development allocate more biomass into their belowground structure in order to reduce a root to shoot ratio and improve water availability (Thomas, Gausling 2000). This can be explained by the substantially larger sizes of sprout aboveground parts compared to seedlings of the same age (Table 1) and low SLA, also confirmed in experiments of Drake et al. (2012) and Pietras et al. (2016). Sprouts do not experience drought to the same extent as shown by our results, the water and nutrients are not limited due to the deep well-developed root system, thus water use efficiency might be greater (Drake et al. 2012) and the photosynthetic apparatus is not limited in assimilation (Stojanović et al. 2016).

CONCLUSIONS

Drought as a major climatic extreme is more and more intensively exhibited under global climate change, particularly during the last decades. The vulnerability of forest trees and stands to drought increases proportionally to drought intensity and duration, and interactions with other stressors. Therefore, appropriate adaptive silvicultural measures are required to be applied in the forest practice. As confirmed by presented results, oak coppice sprouts transpired significantly more during favourable, as well as under water-limiting conditions, particularly during considerable drought in 2015. The more favourable water status confirmed by leaf water potential results suggests better water availability due to the deeper root system, therefore favouring coppices as an advantageous regeneration and management system in areas exposed to drought.

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