Comparison of assimilation parameters of coppiced and non-coppiced sessile oaks

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Coppice forest is an alternative to high forest mainly aimed at the production of firewood with a short rotation period. A new interest in this silvicultural system has arisen with the demand for renewable energy resources. Exploiting the existing root system of the stump, sprouts are advantaged over plants of seed origin, and this advantage could induce changes at the level of a photosynthetic apparatus, especially in young plants. This paper presents a comparison of the photosynthetic ability of young sprouts, young seedlings and mature trees of sessile oak (*Quercus petraea* (Matt.) Liebl.) growing in a forest stand managed as a coppice-with-standards in the southeast of the Czech Republic. The basic photosynthetic characteristics and transpiration rate at the leaf level were determined using gas-exchange measurement techniques. Data taken in non-limiting conditions were compared with those obtained under limiting soil moisture. The results revealed no differences between the measured parameters of sprouts, seedlings and old trees in non-limiting conditions. Contrastingly, sprouts had the highest photosynthetic capacity and transpiration during drought due to their ability to maintain a higher stomatal conductance as compared with seedlings and old trees. This suggests a better drought tolerance of sprouts compared to seedlings.

Keywords: Drought, Photosynthesis, Sprouts, Seedlings

Introduction

The production of sprouts after cutting, damage or dramatic changes in environmental conditions is a common attribute of temperate angiosperm trees (Del Tredici 2001). Coppicing, the oldest type of forest management, induces the sprouting of basal shoots and the fast production of wood without any subsequent silvicultural treatment (Kadavý et al. 2011). Due to the exploitation of the stump root system, sprouts rapidly grow in their first years of life (Dickmann 2006). The height growth rate varies from 0.5 to 1 m per year, depending on many factors, such as the tree species, site conditions, stump age or the timing of cutting (Del Tredici 2001). The sprouting ability of tree species of Central

Europe was investigated by Matula et al. (2012) and Šplíchalová et al. (2012). They reported that the stump sprouting ability of *Quercus petraea* (Matt.) Liebl. decreased with increasing stump diameter and age. Contrariwise, *Carpinus betulus* (L.) and *Tilia cordata* (Mill.) resprouted well from stumps of all diameters. A faster growth rate of sprouts, compared to trees of seed origin, leads to an earlier growth culmination and a shorter rotation period that can range from 5 to 40 years, depending on the purpose. For example, a 5-year rotation period is usually taken for the production of wicker from willow, 15 years for oaks to obtain tan barks and 40 years for fuel production (Cotta 1845). Coppice management provides sustainable production of

thin stems of lower quality (mainly used as firewood) as compared with those from high forests, with a lower financial profit (Fujimori 2001); however, in terms of costs for forest cultivation, coppice is cheaper than high forest (Kneifl et al. 2011).

Interest in coppice management has recently arisen after the claim of the European Union to increase the proportion of energy obtained from renewable resources and to reduce the consumption of fossil fuels (Kuiper et al. 1998). Short-rotation coppices are often established for afforestation of unused agricultural soils and restoration of landfills (Nixon et al. 2001). The most frequently claimed advantage of coppice is an increase in the overall biodiversity of the site, especially in terms of heliophile forest species (Spitzer et al. 2008, Van Calster et al. 2007, Baeten et al. 2009). Due to its low managing costs, coppice seems a valuable alternative for small- and medium-sized-forest owners, as well as for the regeneration of stands where seedling establishment is difficult. For example, fast-growing sprouts can be used for soil stabilization on steep slopes (Roy & Morgan 2011). On the other hand, coppice has several disadvantages compared with high forests, such as the lower quality of timber production, the reduced genetic diversity of sprouts as compared to seedlings, that may lead to a decreased plasticity of the

Tab. 1 - Age and mean values ± standard deviations of basic characteristics of three studied groups of sessile oak measured in 2014 (*n* = 10). (H): plant height; (D$_{0.1}$): sprouts and seedlings stem diameter 10 cm above the ground/stump base; (DBH): the old trees stem diameter at breast height; (LA): plant leaf area.

Group	Age (years)	H (m)	D$_{0.1}$ or DBH (mm)	LA (m^2 plant^{-1})
sprouts	5	2.6 ± 0.4	32.0 ± 6.5	3.2 ± 0.9
seedlings	5	1.7 ± 0.3	15.2 ± 1.8	0.7 ± 0.2
branches	77	17.1 ± 1.2	256.7 ± 36.3	-

stand in terms of response to environmental constraints (Lloret et al. 2004). Moreover, natural regeneration from seedlings can be hampered by sprouts in stands of fast-growing broadleaved species (Vartiamäki 2009). Finally, the more frequent removal of the standing biomass in coppice as compared with high forests may lead to an impoverishment of soil nutrients (Kadavý et al. 2011).

This paper is focused on the comparison under different soil moisture conditions over two growing seasons of the photosynthetic ability and assimilation characteristics of young sprouts, young seedlings and mature trees of sessile oak (*Quercus petraea* (Matt.) Liebl.) growing in a coppice-with-standards forest located in the southeastern Czech Republic. Our starting hypothesis was that young oak sprouts have higher photosynthetic rate due to the possibility of using resources from the existing stump root system (Sakai & Sakai 1998, Von Fircks & Sennerby-Forsse 1998, Lloret et al. 2004, Dickmann 2006).

Material and methods

Site description

The stydy site of Sobešice is located in the southeast of the Czech Republic (49° 14′ 42″ N, 16° 35′ 59″ E, 355 m a.s.l.) in the Training Forest Enterprise Křtiny of the Mendel University in Brno. This site is characterized by a mean annual temperature of 7.5 °C and a mean annual precipitation from 550 to 650 mm. A study area of 200 × 200 m was established in 2009/2010 in a 73-year-old oak forest, where 95% of the total number of trees was sessile oak of predominantly coppiced origin. The stand was characterized by the presence of seedlings naturally regenerated from seeds of left standards and sprouts grown as a multistem coppice from stumps, with an average of 12 sprouts per stump. The area was

divided into 16 square-shaped plots with an area of 2500 m^2 differing in felling intensity, *i.e.*, from clearcut plots (100% of trees harvested) to medium-harvested plots (76% of trees harvested). The aim of the treatment was to convert the existing forest into coppice and coppice-with-standards with different stand density. More detailed description of the conversion procedures is in Kadavý et al. (2011). The different stand density of the plots did not affect assimilation parameters at the leaf level and therefore it was not reflected in this study. In 2014, ten sprouts and ten seedlings were harvested to compare their biometric characteristics. The diameter at breast height (DBH) and tree height of ten old trees were measured for each plot (Tab. 1).

In situ measurement

The *in situ* physiological measurements were carried out during three days of the growing season 2013 (20th June, 1st August, 5th September) and two days of 2014 (17th June, 8th August). Days with different level of drought stress were chosen based on measurements along the growing seasons of the following variables: air temperature (°C) and relative humidity (%), measured using a Minikin RTHi (EMS, Brno, CZ), and precipitation (mm) using a MetOne 380 (EMS, Brno, CZ). Soil temperature at a depth of 1.5 cm and the soil volumetric water content in the range 0-6 cm below the ground surface were monitored during the measuring days using the TPD32 penetrate thermometer (°C – Omega, CZ) and the ThetaProbe ML2x soil moisture sensor (m^3 m^{-3} – Delta-T Devices, UK). Four plants from each group (young sprouts, young seedlings and lower branches of old trees) were randomly selected within the plot. On every plant, a sun-exposed and fully developed leaf without sign of damage was measured at 9:00-12:0 a.m. The measurement was repeated on the same leaf in the

next measuring day of the growing season. Assimilation parameters, such as the light-saturated CO_2 assimilation rate (A_{max}), the stomatal conductance (g_s) and the transpiration rate (E) were measured using a gas-exchange system (LI-6400, LI-COR, USA). The leaves were exposed to the same air flow rate (500 μmol s^{-1}), the ambient CO_2 concentration (400 μmol CO_2 mol^{-1}) and the saturated photosynthetic photon flux density (PPFD, 1400 μmol photons m^{-2} s^{-1} – LI-6400-2 LED light source, LI-COR, USA) in the measuring chamber during all the sampling days. The saturated level of PPFD was chosen high enough so as the CO_2 assimilation rate (A) did not increase further above this level, and the measured leaves were commonly exposed to this level during sunny days. Temperature and air humidity in measuring chamber followed the actual environmental conditions. The relationship between A and the intercellular concentration of CO_2 (C_i, A-C_i response curve) at a saturated PPFD (1400 μmol photons m^{-2} s^{-1}) was recorded. A-C_i response curves were not measured only in the first sampling day (20th June), The A-C_i response curve started at ambient CO_2 concentration (400 μmol CO_2mol^{-1}), decreased stepwise to 200, 100, 50 μmol CO_2mol^{-1} and then increased to 700, 1500 μmol CO_2mol^{-1}. The values of the A-C_i response curves were used for the estimation of the light and CO_2-saturated CO_2 assimilation rate (A_{sat}), the rates of *in vivo* Rubisco carboxylation (V_{Cmax}), electron transport (J_{max}) and triose phosphate utilisation (TPU). The equations of Farquhar et al. (1980) with modification of the Michaelis-Menten constants of Rubisco by Harley et al. (1992) were used for A-C_i response curve analyses.

Statistical analysis

The obtained data were tested for normality and homogeneity of variances. Two-way analysis of variance (ANOVA) was performed to evaluate the differences in the mean values among different groups (sprouts, seedlings and branches), among different date of measurement and their dependence. Differences among means were tested using the Tukey's *post-hoc* test (α = 0.05). All statistical tests were performed using the software package SigmaPlot® version 11.0 (Systat Software, Inc., USA).

Results

The drought conditions occurred in August 2013 and June 2014 were characterized by low soil volumetric water content (less than 10 m^3 m^{-3}) and a high vapor pressure deficit (VPD). The drought in August 2013 was accompanied by higher temperature as compared with June 2014 (Tab. 2). The dry weather induced a significant reduction in g_s (Fig. 1) and an increase in the limitation of CO_2 diffusion into the leaf, as revealed by the decreasing ratio between the intercellular and air CO_2 concentrations (C_i/C_a - Fig. 1). The low g_s also caused a

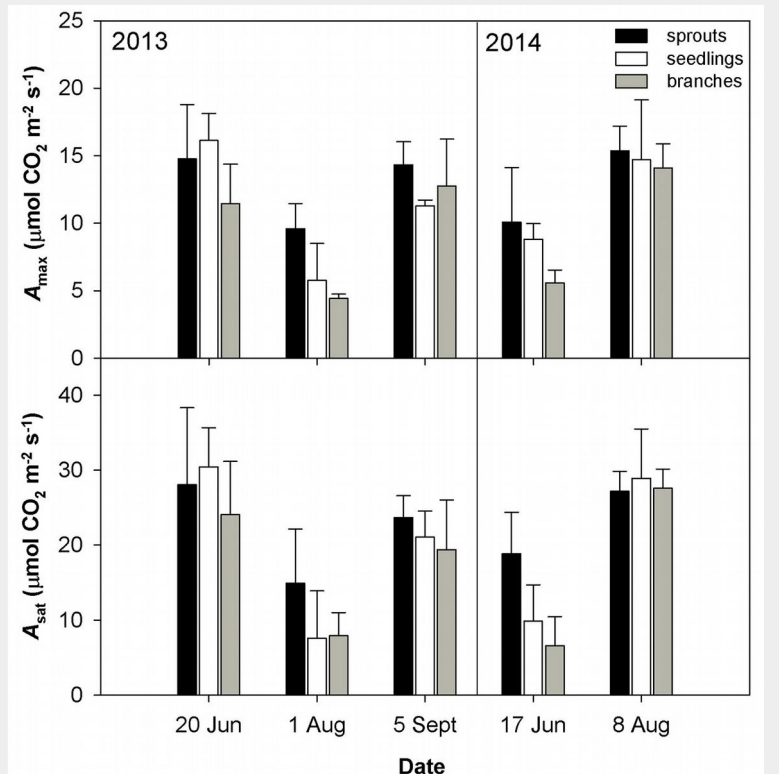**Tab. 2** - Mean values ± standard deviations of soil volumetric water content (SWC, *n* = 60), soil temperature (T_s, *n* = 60), vapor pressure deficit based on leaf temperature (VPD, *n* = 12) and leaf temperature (T_L, *n* = 12) measured in 2013 and 2014.

Date	SWC (m^3 m^{-3})	T_s (°C)	VPD (kPa)	T_L (°C)
20 Jun 2013	21.4 ± 6.2	27.1 ± 2.4	1.6 ± 0.2	34.7 ± 0.8
1 Aug 2013	8.0 ± 1.7	26.6 ± 3.7	2.2 ± 0.3	30.5 ± 0.7
5 Sept 2013	14.7 ± 3.2	20.7 ± 1.9	1.3 ± 0.1	25.3 ± 0.8
17 Jun 2014	7.2 ± 1.4	18.4 ± 1.5	2.0 ± 0.2	24.9 ± 0.7
8 Sept 2014	17.3 ± 3.8	20.9 ± 1.9	1.5 ± 0.2	28.4 ± 0.7

Fig. 1 - Mean values ± standard deviations ($n = 4$) of stomatal conductance (g_s) measured under ambient CO_2 concentration 400 μmol CO_2 mol^{-1}, ratio between intercellular and air CO_2 concentration (C_i/C_a) and transpiration rate based on gas exchange measurement (E) in 2013 and 2014 conducted on three studied groups (sprouts, seedlings and lower branches of old trees) of sessile oak.
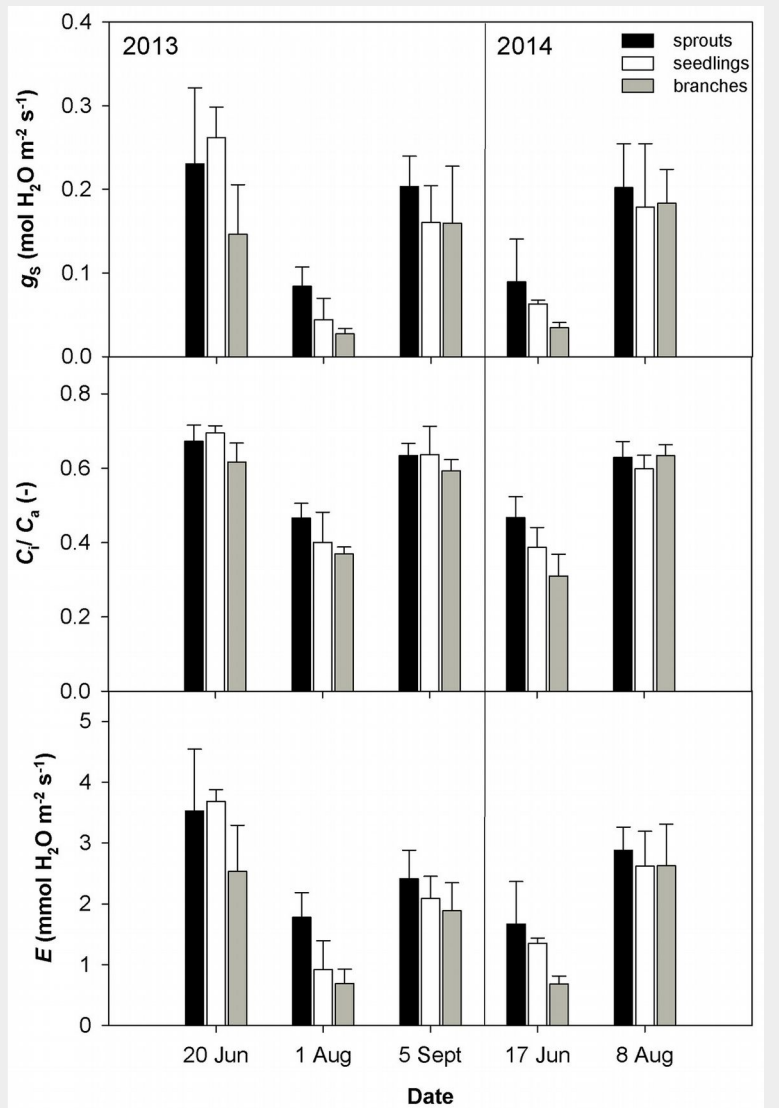
Fig. 2 - Mean values ± standard deviations ($n = 4$) of light-saturated CO_2 assimilation rate (A_{max}) and light- and CO_2-saturated CO_2 assimilation rate (A_{sat}) during two years of measurements conducted on three studied groups (sprouts, seedlings and lower branches of old trees) of sessile oak.
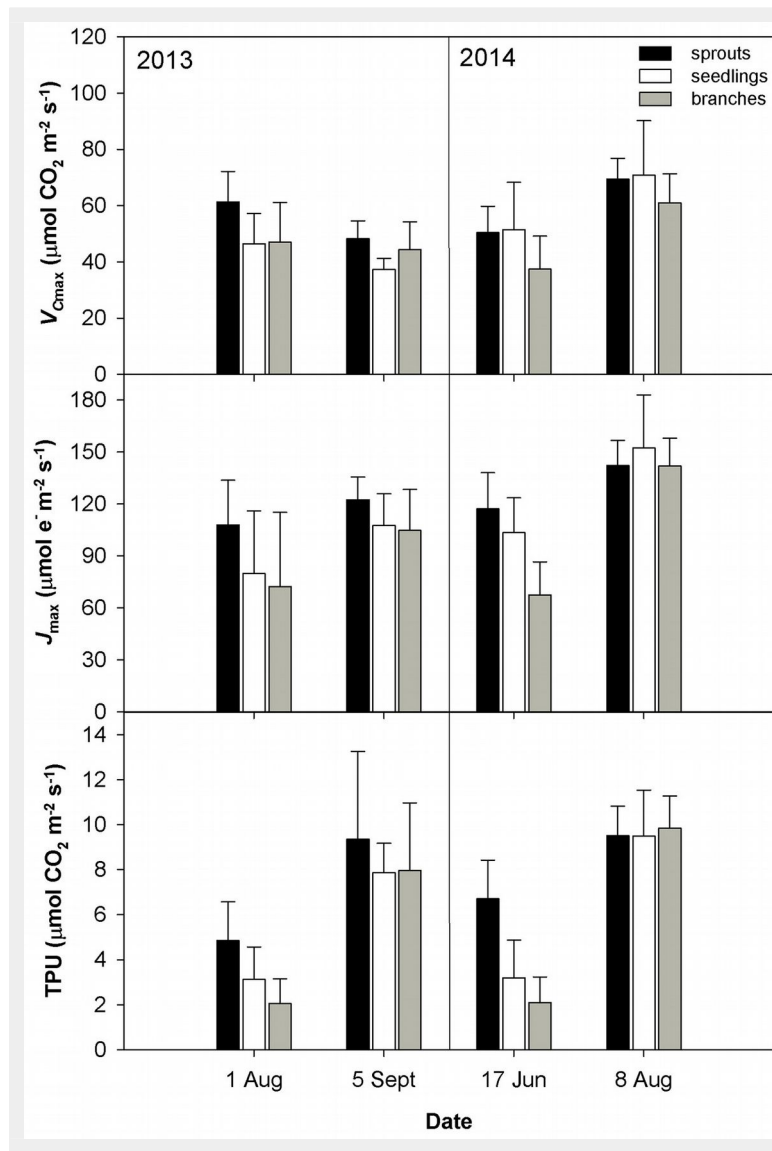
Fig. 3 - Mean values ± standard deviations ($n = 4$) of *in vivo* Rubisco carboxylation rate (V_{Cmax}), electron transport rate (J_{max}) and rate of triose phosphate utilisation (TPU) during two years of measurements conducted on three studied groups (sprouts, seedlings and lower branches of old trees) of sessile oak.

decline in E (Fig. 1). The drought conditions brought about a reduction in the CO_2 assimilation rate (A_{max}, A_{sat} - Fig. 2). A_{max} and A_{sat} were lower in the hot and dry August 2013 than in the dry June 2014. The V_{Cmax} seemed not to respond to drought in 2013. In 2014, V_{Cmax} was approximately 23-39% lower in June than in August (Fig. 3). J_{max} was reduced by drought in both years; however, its reduction was significant only in 2014 (Fig. 3). The rate of utilization of the created triose phosphates (TPU) de-creased during drought more than J_{max} and V_{Cmax}. The reduction of TPU was approximately 29-79 %, the lowest being in sprouts and the highest in branches (Fig. 3).

The A-C_i response curves in the hot and dry days of August 2013 showed a reversed
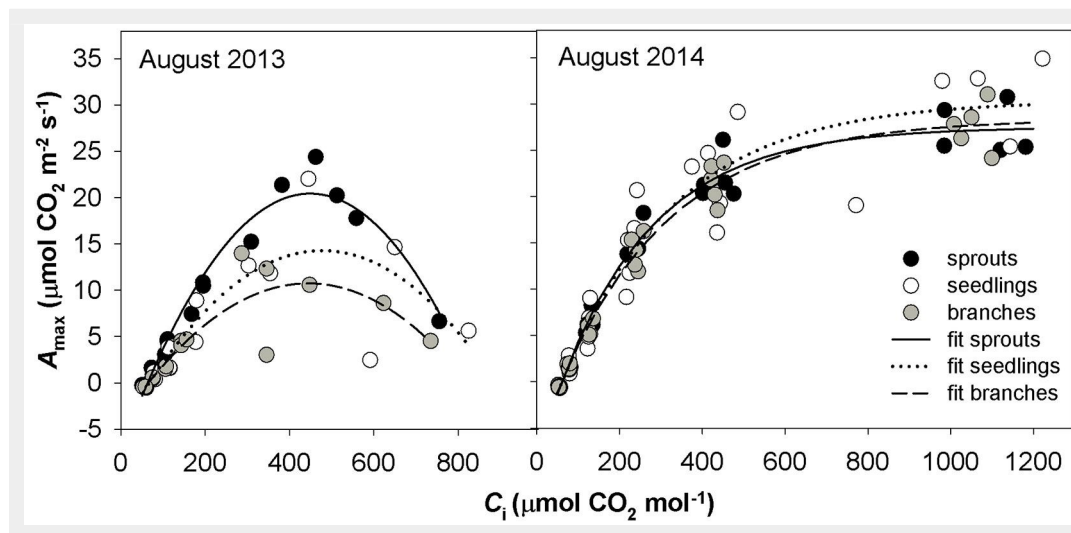
Fig. 4 - The relationship between light-saturated CO_2 assimilation rate (A_{max}) and intercellular CO_2 concentration (C_i) under drought in August 2013 and in moisture-nor-mal August 2014 in three studied groups of sessile oaks. The graphs indicate individual measured val-ues and their fits.

Fig. 5 - The relationship between CO_2 assimilation rate (A) and stomatal conductance (g_s), *in vivo* Rubisco carboxylation rate (V_{Cmax}), electron transport rate (J_{max}) and rate of triose phosphate utilisation (TPU). The individual measured values are divided in A measured under light-saturated and drought-unaffected condition (A_{max}) and drought affected condition (A_{max}-drought), A measured under light- and CO_2-saturated and in drought-unaffected condition (A_{sat}) and drought affected condition (A_{sat}-drought). Quadratic and linear function were used to fit data; the coefficients of determination from regression analysis are shown near to the corresponding curve.
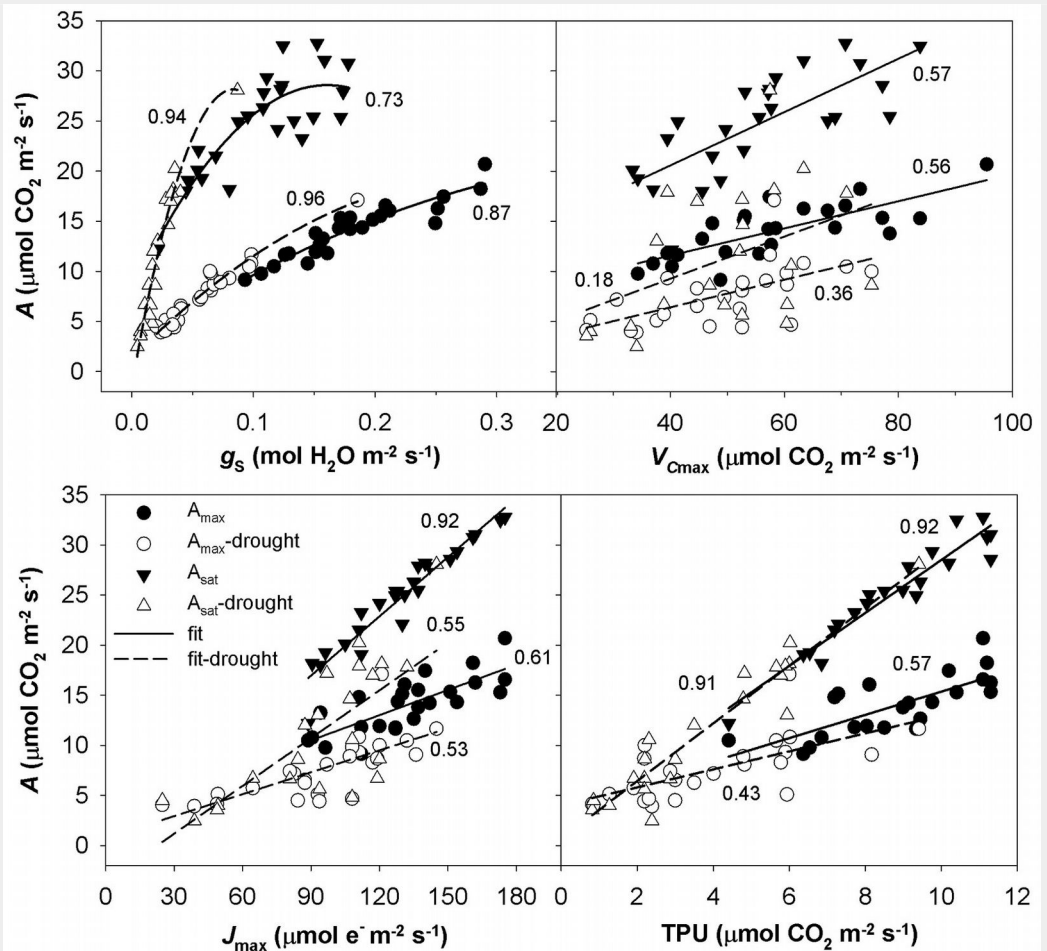
sensitivity to C_i, *i.e.*, the rate of photosynthesis did not increase with increasing C_i to a saturated value as for August 2014, but reached a maximum value and started to decrease (Fig. 4). The A-C_i response curves measured in September 2013 were similar to those taken in August 2014. Not all A-C_i response curves observed for June 2014 showed a reversed sensitivity to C_i as in the case of August 2013. To understand which process controls the photosynthesis, a pairwise correlation analysis using the parameters A_{max}, A_{sat} and g_s, J_{max}, V_{Cmax} and TPU was conducted (Fig. 5). A_{max} resulted tightly correlated with g_s, while A_{sat} was correlated with g_s only in the case of drought-affected values. A_{max} and A_{sat} showed moderate dependence on V_{Cmax} only in drought-unaffected months. A high correlation was found between drought-unaffected A_{sat} and J_{max}. Both drought-affected and drought-unaffected A_{sat} highly depended on TPU.

Differences in the measured parameters between sprouts, seedlings and lower branches of mature trees were low in the non-dry parts of the growing season (June and September 2013, August 2014). However, such differences increased under drought (August 2013 and June 2014) regardless of the time along the growing season. Under drought conditions, sprouts usually showed the highest values of the studied parameters, and the branches showed the lowest. The greatest differences between the studied groups were found for A_{sat}, TPU, g_s and the lowest for V_{Cmax} (Fig. 1, Fig. 2, Fig. 3).

Discussion

Our starting hypothesis that young oak sprouts have higher photosynthetic activity as compared to other groups was not confirmed; however, sprouts showed some indication of better coping with drought stress.

Compared with seedlings, sprouts are characterized by a faster above-ground growth during early development (Herve & Ceulemans 1996, Liberloo et al. 2009, Drake et al. 2012), although this does not entails a higher photosynthetic ability of sprouts. Indeed, seedlings allocate more assimilated carbon to below-ground biomass and root development than plants from coppicing (Drake et al. 2009). Therefore, seedlings can have the same or even a higher photosynthetic rate than sprouts, though their above-ground growth can be smaller (Drake et al. 2009).

In this study, significant differences in the measured assimilation parameters among sprouts, seedlings and branches of mature trees were observed only during periods of drought. Decreased CO_2 diffusion from the atmosphere to the site of carboxylation due to stomatal closure is generally considered the main cause for decreased photosynthesis under mild to moderate water deficit (Chaves et al. 2003, Flexas et al. 2006). Different g_s under drought between sprouts and seedlings can be caused by different root absorptive area and root depth. Under drought conditions, sprouts benefit from the developed root system, that allows a higher water uptake than that of seedlings (Lloret et al. 2004). A lower water limitation and a higher water potential of sprouts compared to seedlings was also confirmed in studies describing the effect of drought after wildfire on seedlings and sprouts survival (Williams et al. 1997, Clemente et al. 2005). A higher g_s allowed the sprouts to maintain a higher rate of use of the assimilates, which led to a lower down-regulation of photosynthesis compared to that of seedlings and branches of old trees. Lower branches of old trees had the lowest g_s during drought. It is known that g_s usually declines with tree height and age, due to longer hydraulic pathways and an increase in the leaf-area-to-sapwood-area ratio (Steppe et al. 2011). A greater reduction in the stomatal conductance in leaves of large trees can be observed during drought in comparison with young plants. Moreover, many sprouts on a single stump (as in our study) may create a more favorable microclimate

by self-shading sprouts, thus overcoming hot and dry weather. Drake et al. (2009) tested the hypothesis that the disproportionate amount of below-ground biomass in coppices can change the leaf-to-air vapor pressure difference or intrinsic water-use efficiency when compared to those of seedlings, but no differences were observed.

Water deficit can diminish the photosynthesis close to zero without a decline in photosynthetic capacity (A_{sat}). Down-regulation of A_{sat} occurs when drought stress is too high or accompanied by another stress, such as high PPFD or heat stress (Chaves 1991). In the present study, drought occurred with high PPFD and high temperature, especially in August 2013, when A_{sat} was mostly down-regulated. In such cases the products of photochemical reaction overcomes the capacity for their utilization and insufficient inorganic phosphate (P_i) regeneration limits ATP production that affects electron transport and RuBP regeneration (Harley & Sharkey 1991). Regression analysis showed that A_{sat} was dependent on J_{max} and TPU under drought-unaffected condition. Drought led to the disappearance of A_{sat} dependence on J_{max}, but dependence on TPU remained and dependence on g_s was developed (Fig. 5), although this relationship is unusual during measurements in high C_i. These conditions led to atypical course of A-C_i response curves, especially in August 2013 (Fig. 4). Harley & Sharkey (1991) explained the reversed sensitivity of photosynthesis to C_i by suppressed photorespiration in high C_i that does not allow P_i regeneration in chloroplasts, which would lead to alleviation of P_i-limitation. Response of plant to drought is very complex process and stomatal closure is not the only regulatory mechanism of photosynthesis. A water deficit reduces the flow rate in the phloem and also reduces the movement of assimilates from mesophyll (Ruehr et al. 2009). The recent assimilates are accumulated in source leaves, the rate of triose phosphates utilization is reduced and can be followed by down-regulation of the assimilation capacity. Stomata can respond to changes in mesophyll metabolism, so their dependency on assimilation capacity can be observed (Farquhar & Sharkey 1982).

Conclusion

Although sprouts had a greater aboveground biomass than seedlings of the same age, their photosynthetic ability at the leaf level was not higher than that in seedlings or old trees in water non-limiting conditions. On the other hand, a larger root system of sprouts, as compared to seedlings, likely enabled them to maintain a higher stomatal conductance during drought and led to a lower down-regulation of CO_2 assimilation. This study showed better drought tolerance of sprouts compared to that of seedlings.

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