Diurnal photosynthetic performance of two oak species from two provenances in a Mediterranean and a central European common garden


Abstract

Oaks may contribute to the stabilization of European forests under climate change. We utilized two common gardens established in contrasting growth regimes, in Greece (Olympiada) and Germany (Schwanheim), to compare the diurnal photosynthetic performance of a Greek and an Italian provenance of two Mediterranean oaks (Quercus pubescens and Q. frainetto) during the 2019 growing season. Although the higher radiation in the southern common garden led to a strong midday depression of chlorophyll 𝛼 fluorescence parameters (maximum quantum efficiency of PSII, performance index on absorption basis), comparable light-saturated net photosynthetic rates were achieved in both study areas. Moreover, both species and provenances exhibited analogous responses. Q. pubescens had enhanced chlorophyll 𝛼 fluorescence traits but similar photosynthetic rates compared to Q. frainetto, whereas the provenances did not differ. These findings indicate the high photosynthetic efficiency of both oaks under the current climate in Central Europe and their suitability for assisted migration schemes.

Keywords: assisted migration; chlorophyll fluorescence; diurnal variation; gas exchange; Quercus frainetto; Quercus pubescens.

Introduction

The anthropogenic climate change leads to increasing average temperature and altered precipitation patterns all over the world. The global surface temperature was 1.09°C higher in 2011–2020 than that in 1850–1900 (IPCC 2021). In Western and Central Europe, as well as in the Mediterranean area, summer heat and drought events are increasing in frequency, duration, and intensity, as had been foreseen (García-Ruiz et al. 2011, Hoegh-
Gulder et al. 2018, Spinoni et al. 2018). Based on the anticipated altitudinal and latitudinal shift of climate zones from the equator poleward (Loria et al. 2009), vegetation dynamics models predict a parallel shift of plant species distribution from South to Central Europe (Hickler et al. 2012). Shifting species distribution limits have also been reported in Mediterranean forests due to intensified drought and related tree mortality (Vayreda et al. 2016, Dorado-Liñán et al. 2019, Zindros et al. 2020). Plant species movement takes place along a climatic gradient, from limited water availability at lower altitudes to a low-temperature threshold at higher altitudes or latitudes (Babst et al. 2013). However, the slow migration potential and the long regeneration time of forest ecosystems make them particularly prone to environmental variability (Vitt et al. 2010).

Summer droughts associated with extreme heat waves and lack of precipitation already occurred in Central Europe in 2003, 2018, and 2019, and in southern Europe in 2017 and 2021, and their consequences were evident in forest ecosystems, such as the increase in desiccation damages, insect disturbances, and acceleration in tree decline and mortality in Europe (e.g., Brèda et al. 2006, Seidl et al. 2017, Puletti et al. 2019). Hanewinkel et al. (2013) suggest that by 2100, between 21 and 60% of European forest land will be suitable only for Mediterranean oak forest types, but natural migration processes lack the speed to keep on track with climate change. To counteract the shrinking forest cover and the onset of desertification processes, drastic management interventions, such as assisted migration, are necessary to stabilize threatened forest ecosystems (Bussotti et al. 2015). Assisted migration is the human-assisted movement of species to habitats that they otherwise cannot currently colonize. It can be applied when it is predicted that a threatened habitat will in the future have the same climate as the current habitat of the target species and it can be separated into three approaches: assisted population migration, assisted range expansion, and assisted long-distance migration (Winder et al. 2011).

Oaks are prioritized for assisted migration, due to their advantageous traits; they are characterized by high tolerance to light and drought stress, are less impacted by photoinhibition, in comparison to other Mediterranean woody species (Valladeres et al. 2005), and have higher phenological plasticity and adaptation potential to climate change than other broadleaf species (Wenden et al. 2019). Quercus pubescens Willd. and Quercus frainetto Ten. are native to Greece, where they grow in the entire country (Strid and Tan 1997). On the contrary, Q. frainetto is not native to Germany and Q. pubescens is found only in limited locations in SW Germany (Bussotti et al. 1998, Pasta et al. 2016). Introducing seed material of these oak species from an Italian provenance in Greece would be equivalent to the approach of assisted population migration to enlarge the gene pool of the already existing species (Winder et al. 2011). The attempt to establish the species in central European ecosystems (e.g., in Germany) corresponds to the approach of assisted range expansion, which imitates natural migration processes, but is unlikely to occur at the velocity of climate change due to landscape fragmentation (Vitt et al. 2010, Winder et al. 2011) or slow migration speed of the target species. To test the performance of these oak species, coming from different regions of the Mediterranean area, from the perspective of assisted migration, a replicate common garden experiment has been established (Bantis et al. 2021). In a common garden experiment, two or more species and different provenances are transplanted to a common environment to allow their more direct comparison. Such trials of provenances of different forest species are a valuable tool for assessing both species and provenances’ adaptive potential to changing environments (e.g., Stojnić et al. 2015, Pollastrini et al. 2020).

Although both studied species are extensively distributed in the Mediterranean region (Euro+Med 2006), they differ in their ecophysiological responses to xerothermic conditions. Q. frainetto is generally regarded as less drought-resistant compared to Q. pubescens, as quite a low leaf water potential levels cannot be avoided even with almost complete stomatal closure during severe drought (Fotelli et al. 2000, Siam et al. 2009). Consistently, lower photosynthetic rates, water-use efficiency, predawn leaf water potentials, and finally, growth and survival are reported for Q. frainetto vs. Q. pubescens (Bantis et al. 2019, 2021; Pollastrini et al. 2020). The higher drought sensitivity of Q. frainetto is also indicated by changes in chlorophyll fluorescence parameters, such as a decline of the performance index PI_{abs} (Bantis et al. 2019). The more advantageous responses of Q. pubescens can be partially attributed to the extensive root system that the species develops to exploit water from deeper soil layers (Früchtenthal et al. 2018). Furthermore, the two species differ in the length of their growing period. Their differences in terms of drought and frost tolerance affect the onset of leaf senescence, with Q. frainetto showing a shorter leaf life span than Q. pubescens (Holland et al. 2014, 2016; Koller et al. 2020).

In the present study, we used a common garden experiment established in Greece and Germany, with Greek and Italian provenances of Q. frainetto and Q. pubescens seedlings, to assess the responses of the two species and provenances under different growth regimes induced by latitudinal and microclimatic differences. This approach will enhance our understanding of their potential for assisted population migration and range expansion in the face of the declining vitality of the local oak forests (discussed, e.g., in Süßel and Brüggemann 2021). We measured different photosynthetic performance indicators, such as chlorophyll fluorescence and gas-exchange parameters, and focused on the diurnal course of these traits as, to our knowledge, limited information is available about their diurnal variation in Mediterranean oaks (Ogaya and Peñuelas 2003, Siam et al. 2008) or oaks grown at Mediterranean-type ecosystems (Matzner et al. 2003). Our hypotheses were that (1) Q. pubescens would exhibit more efficient photosynthetic activity than that of Q. frainetto on both sites, based on its lower drought sensitivity, and (2) the Greek provenances of both species would outperform the Italian ones in Greece, whereas the Italian provenances would be more suitable in Germany,
as climate differences between Germany and Italy are less pronounced as between Germany and Greece.

Materials and methods

Site description and plant material: The measurements were performed in oak seedlings of an existing common garden experiment, established within the FutureOaks project (more details given by Bantis et al. 2021). In this project, Mediterranean oaks of identical accessions were evaluated for their potential as alternative tree species for altitudinal and latitudinal assisted migration. In each common garden, saplings of *Q. pubescens* and *Q. frainetto* were grown from seed material of two provenances: from Northeastern Greece and Central Italy (*Q. pubescens*: Greece 40°35’45”N, 23°45’22”E, 30 m a.s.l., Italy 43°25’02”N, 10°52’25”E, 325 m a.s.l.; *Q. frainetto*: Greece 40°29’30”N, 23°37’51”E, 530 m a.s.l., Italy 41°18’02”N, 13°02’54”E, 25 m a.s.l.).

The common gardens are located in the municipal forest of Frankfurt, in Schwanheim, Germany (SWA, 50°04’12.6”N, 08°33’42.2”E, 114 m a.s.l.), Olympia, Chalkidiki, Greece (OLY, 40°36’33.6”N, 23°45’05.0”E, 48 m a.s.l.). The SWA plantation is situated in an oak and pine site, where forests exist for at least 500 years, on fluvial sand with about a 2-m deep groundwater table. The OLY plantation is established at a former grazing site embedded in a natural *Q. ilex* and *Q. pubescens* forest stand with loamy soil. Water was solely provided by precipitation at both sites. Climate parameters for SWA were recorded on-site with iMetos sm SMT280 weather stations (Pessl Instruments, Weiz, Austria). Climate data for OLY were recorded at the closest weather station of Hellas Gold SA (OAM21), at 40°35’40.07”N, 23°46’5.7”E, 17 m a.s.l.

The measurements took place at the beginning, the middle, and the end of the 2019 growing season (Germany: 24 June 2019, 21 August 2019, 11 September 2019; Greece: 18 May 2019, 30 July 2019, 9 October 2019). The time points of the measurements in Germany were planned according to Koller et al. (2020), who studied the seasonal variability of the SPAD chlorophyll content values of the investigated species planted under the climate conditions in Germany. In each country, measurements were conducted on three two-year-old saplings of each provenance and each species.

Gas-exchange measurements: During each measurement day, light-saturated net photosynthetic rates (*P*<sub>max</sub>) and stomatal conductance (*g*) were measured on the same two leaves per selected plant using the LI6400XT portable gas-exchange analyzer coupled to a LI6400-40 fluorescence chamber (LiCor, Nebraska, USA). Fully expanded, optically healthy, sunlit leaves were placed in the chamber, fully covering the 2-cm<sup>2</sup> cuvette and the cuvette was firmly closed to ensure stable measurements. Photosynthetically active radiation (PAR) was set at 1,000 μmol(photon) m<sup>-2</sup> s<sup>-1</sup>, based on the gas-exchange measurements performed at the beginning of the growing season, which showed that light-saturated maximum photosynthesis was achieved at this PAR level. Although PAR may vary seasonally and daily, we chose to keep the same PAR level throughout the study for comparability reasons, consistent with Fotelli et al. (2020). The CO<sub>2</sub> flow rate in the chamber was set to 300 μmol s<sup>-1</sup>, reference CO<sub>2</sub> at 400 ppm, and chamber temperature was set to ambient air temperature. Measurements were performed between 6:30 and 22:00 h, and they were repeated every two hours. The starting and ending time points of measurements differed between seasons and countries following seasonal and latitudinal fluctuations in light daytime duration. The measurements started two to three hours after nautical dawn and were finished before nautical dusk. Intrinsic water-use efficiency was calculated by the ratio of *P*<sub>max</sub> to *g*.

Photosystem II Chl fluorescence: Measurements were conducted on the same leaves used for gas-exchange measurements, plus a third leaf was used for internal control. Immediately after the photosynthesis measurements, leaves were dark-adapted for a minimum of 30 min. PSII functionality was assessed by the JIP test with a portable fluorimeter measure with red light (Handy-PEA, Hansatech, King’s Lynn, UK), using the 50 μs fluorescence level as F<sub>0</sub> according to Strasser et al. (2000, 2004). Although recent studies showed a better fitting of earlier F<sub>0</sub> values to extrapolated ‘true’ F<sub>0</sub> (e.g., 20 μs; Padhi et al. 2021), we chose to use 50 μs as F<sub>0</sub> to enable comparability with previous investigations on the same oak species (e.g., Bantis et al. 2019, 2020, 2021; Koller et al. 2020).

The datasets were analyzed with the PEA Plus 1.0.0.1 software and the Biolyzer software (version 3.0, Ronald M. Rodriguez, Bioenergetics Lab. Geneva, Switzerland) and then further processed with Microsoft Excel (Microsoft® Excel® for Microsoft 365 MSO, version 2110). For the diurnal measurements, the maximum quantum yield of primary photochemistry: ϕ<sub>P<sub>0</sub> (F<sub>V/F<sub>0</sub> </sub>) and the performance index on an absorption basis [PI<sub>abs</sub> = 10 RC/ABS ϕ<sub>P<sub>0</sub> (1 – ϕ<sub>P<sub>0</sub> ψE<sub>o</sub>/(1 – ψE<sub>o</sub>))] measured in samples in the dark-adapted state, were used. These two fluorescence parameters are commonly used to describe changes in PSII performance of the photosynthetic apparatus due to early stress or senescence. Per the measuring campaign, night measurements were additionally conducted to examine in more detail the individual components of the PI<sub>abs</sub> (Fig. 1S, supplement).

Data analysis: Measurements of the same species/provenance/site within each two-hour time window were averaged. Statistical analyses were performed using the GraphPad PRISM 5.0 (GraphPad Software, San Diego, California, USA). Differences between the different sites/seasons/provenances/species were calculated by using the Mann–Whitney’s U-test and statistical differences within groups at different times of the day were calculated using the Kruskal–Wallis test with a Dunn’s multiple comparison post-test. If the number of repetitions per measurement was too low, the statistical evaluation was dispensed with. Corresponding points have been marked by n.a. Principal
Component Analysis (PCA) were run with OriginPro ver. 2021b (OriginLab Corporation, Northampton, MA, USA). Only components with eigenvalues > 1 were loaded.

Results

Climatic conditions during the study: Climate data of the two common gardens during 2019 are outlined at daily resolution (Fig. 1A,B). The mean air temperature was comparable between the two sites. However, air temperature presented greater oscillations during the day in the German common garden, compared to the Greek one, evidenced by more pronounced differences between maximum and minimum daily temperatures.

At SWA, the lowest temperature occurred at the end of January with a minimum air temperature of –11.9°C on the day of the year (DOY) 22 (Fig. 1A). Until the end of March, frost events were frequent. In April and May, only a few frost events occurred and the last one took place in the middle of May (DOY 135). The highest air temperature recorded in 2019 was 42.8°C at the end of July, whereas the highest temperature during the measuring days was 40.4°C. Annual precipitation was 554.8 mm and the sum of precipitation from May to October was 334.4 mm. Air temperature in SWA presented strong fluctuations and the largest difference between the minimum and maximum air temperature was 29.4°C at the end of June (DOY 181).

At OLY, frost occurred only at the beginning of January with a minimum temperature of –5°C (DOY 8, 9). The highest maximum temperature was 38.2°C, which was recorded during the measuring days in July. Annual precipitation was 179.4 mm and precipitation from May to October was 37.4 mm, both far lower than the respective values in SWA. From mid-July until mid-September there was a complete lack of rainfall.

PSII chlorophyll fluorescence: As expected, $\varphi_{P_0}$ and $P_{max}$ values were significantly higher in the German compared to the Greek common garden, in response to the different growth regimes of the two sites. The difference in maximum quantum efficiency of reduction of $Q_A$ ($\varphi_{P_0}$) between the sites peaked at 13:30–15:30 h (Fig. 2A). Only small differences between species were observed. $Q. pubescens$ presented significantly higher values of $\varphi_{P_0}$, compared to

![Fig. 1. Air temperature [°C] (A,B), daily sum of precipitation [mm] (C,D), and daily sum of solar radiation [W m$^{-2}$] (E,F) of SWA – Germany (left) and OLY – Greece (right) in 2019. Daily minimum (grey line) and maximum (dashed line) air temperatures are indicated on the scale above and below the mean daily air temperature (black line). Precipitation and solar radiation per day are also shown as the black line. Measurement dates are indicated by dashed vertical lines.](image)
Q. frainetto only twice during the day (Fig. 2B). Consistent with φP₀, PIₐrgb values were on average 48 ± 10 units higher in the German than in those in the Greek common garden (Fig. 2D). Q. pubescens showed significantly higher PIₐrgb almost throughout the day, except at the beginning and the end of the measurements. The differences between the provenances were less pronounced, as PIₐrgb of the Greek provenance were significantly higher than that of the Italian provenance only from 09:30 h till 13:30 h.

When the chlorophyll fluorescence traits are observed at different time points during the growing season (Fig. 3), the drop of φP₀ and PIₐrgb at midday was visible only in the early growing season in both oak species. Moreover, none of the chlorophyll a fluorescence parameters differed substantially between the species. There was a tendency of PIₐrgb to be higher in Q. pubescens than in Q. frainetto (Fig. 3D–F), but the difference was not significant in most of the tested time points.

Predawn measurements in the early growing season (Fig. 1S) differed 2-fold (PIₐrgb, φP₀: p<0.0001) between the two common gardens. On both sites, the PIₐrgb values of both provenances of Q. pubescens were higher than those of Q. frainetto at all stages of the growing season, due to increased 10RC/ABS and ψE values. In SWA, φP₀ values decreased significantly in Q. frainetto from the early to the mid-stage of the growing season. In Q. pubescens, ψE and PIₐrgb increased significantly from the early to the late stage of the growing season. In OLY, except φP₀ in Q. pubescens, no significant differences were observed between the early and mid-stage of the growing season.

Gas-exchange parameters: Fig. 4 presents the diurnal variation of Pₙmax, gₛ, and WUE between the different sites (Fig. 4A,D,G), species (Fig. 4B,E,H), and provenances (Fig. 4C,F,I). At the Greek common garden, the highest rates of Pₙmax and gₛ were recorded early in the morning and declined thereafter. On the contrary, at the German site, these parameters peaked around 10 h as generally expected. Pₙmax was significantly higher at OLY vs. SWA only early in the morning and between 13:30 h and 15:30 h (Fig. 4I), whereas no significant differences in gₛ and WUE were detected between the two sites. Nevertheless, WUE tended to be higher in OLY during the warmest daily hours, from 10:00 to 14:00 h (Fig. 4G).

At the species level, the highest Pₙmax and gₛ values were recorded early in the morning, between 7:30 and 9:30 h. Comparison among the species revealed no significant difference between Q. frainetto and Q. pubescens in any of the studied gas-exchange traits (Fig. 4B,E,H). The Italian provenances outperformed the Greek ones in terms of Pₙmax and gₛ, only early in the morning, but the difference became smaller and insignificant later on (Fig. 4C,F,I). The differences in gas-exchange traits during the growing season are presented in Fig. 5. The midday depression of Pₙmax and gₛ was observed mainly in the mid-growing season and less in the early growing season, but not at the end of the growing season (Fig. 5A–F). Both species presented their highest Pₙmax values early in the day, in the middle of the growing season (Fig. 5A–C). Despite its decrease in autumn, a considerable Pₙmax was still measured in autumn (Fig. 5C). Then, the greatest gₛ values were recorded (Fig. 5F). Regardless of these seasonal fluctuations, no clear differences were detected.
Fig. 3. Diurnal course of the maximum quantum efficiency of reduction of $Q_A$ ($\Phi_{P_0}$) (A–C) and the performance index on an absorption basis ($\text{PI}_{abs}$) (D–F), measured at three dates per species (early, mid, and late stage of the growing season) shown as mean values ± SE ($n = 2–21$). Statistically significant differences between the species are shown by asterisks with significance levels at 5% (*), 1% (**), 0.1% (***) , and 0.01% (****), or n.a. when not applicable, respectively.

Fig. 4. Diurnal course of light-saturated net photosynthetic rate ($P_{\text{Nmax}}$), stomatal conductance ($g_s$), and water-use efficiency (WUE), shown as mean values ± SE. Data are grouped and compared site-wise (A,D,G) SWA/OLY; $n = 5–43$, species-wise (B,E,H) $Q. \text{frainetto}/Q. \text{pubescens}$; $n = 2–43$, and provenance-wise (C,F,I) Italian/Greek; $n = 5–47$. Statistically significant differences between the groups are shown by asterisks with significance levels at 5% (*), 1% (**), 0.1% (***) , and 0.01% (****), or n.a. when not applicable, respectively.
between the two oak species. *Q. pubescens* vs. *Q. frainetto* tended to exhibit higher $P_{\text{Nmax}}$ and WUE in the late- and mid-growing season (Fig. 5C,H), respectively, but in most of the cases these differences were not significant.

**Discussion**

Over the course of the growing season, the capacity of a plant’s photosynthetic performance changes. A gradual increase in chlorophyll content and photosynthesis and gradual changes in chlorophyll $a$ fluorescence-related parameters are observed with leaf development (Jiang et al. 2006, Koller et al. 2020). Several studies combined the measurement of chlorophyll $a$ fluorescence traits with gas-exchange parameters for a comprehensive assessment of the photosynthetic apparatus and the associated changes in stomatal function in different oak species (e.g., Epron et al. 1992, Valladares et al. 2005, Siam et al. 2009, Pollastrini et al. 2020). In our study, we analyzed the parameters $\varphi_{\text{P}}$ and $\text{PI}_{\text{abs}}$ to check how photosynthetic performance changes during the growing season over the day and with actually measured photosynthetic rates. Both parameters are the two most commonly used chlorophyll $a$ fluorescence parameters to monitor and identify species-specific stress tolerance responses. Whereas $\varphi_{\text{P}}$ reflects only the maximum quantum yield of (mainly) PSII primary photochemistry ($F_{\text{v}}/F_{\text{m}} = \varphi_{\text{P}}$; Strasser et al. 2000, 2004) and is widely used to estimate the degree of photoinhibition (Tezara et al. 2005), the $\text{PI}_{\text{abs}}$ is suitable for gaining a better overview of the whole process in the electron transport chain by incorporating also two other components of the electron transport, besides $\varphi_{\text{P}}$: RC/ABS reflecting the active reaction centers on absorption base, and $\psi_{\text{E}}$, expressing the probability that an absorbed photon leads to a reduction further than $Q_{\text{A}}$ (Strasser et al. 2000, 2004). Additionally, $\text{PI}_{\text{abs}}$ vs. $\varphi_{\text{P}}$ is more sensitive to various stressors, such as decreasing leaf water content, and is therefore often used as a general fitness parameter (Jednowski et al. 2014, 2015).

**Midday depression and seasonal variability:** A clear depression of $\varphi_{\text{P}}$ and $\text{PI}_{\text{abs}}$ at midday and recovery in the evening were observed in the southern (OLY) common garden (Fig. 2A,D), particularly at the beginning of the growing season (Fig. 3S, *supplement*). Such a pattern was evident in the northern SWA only in $\text{PI}_{\text{abs}}$ during the early growing season in June, near the summer solstice, when radiation and temperature were the highest of the year (Fig. 1). This midday depression of both chlorophyll $a$ fluorescence traits was also exhibited by both studied oak species (Fig. 3A,D), in line with reported literature on a wide range of plant genera (e.g., Demmig-Adams...

A midday depression, although less intense, was also detected in both oaks for $P_{\text{max}}$ and $g_*$ in the early and mid-growing season, but not at the end of the growing season (Fig. 5). Midday depression of photosynthesis can be attributed to both stomatal and nonstomatal limitations in response to light stress and stress imposed by high temperatures and VPD (e.g., Epron et al. 1992, Zhang and Gao 1999). However, the conditions that caused these patterns were different in the early and mid-growing seasons. Early in the growing season, the rapid recovery of the systems with increased $\varphi_P$ and $P_{\text{max}}$ values towards the evening and higher values during the night (Fig. 1S) speaks for a dynamic protection process. This could be achieved either by dynamic photoinhibition including resynthesis of the D1 protein (Krause et al. 1993) or by a temporary downregulation mechanism of PSII like an increase in dissipation of excitation energy as heat (Epron et al. 1992, Long et al. 1994). Brüggemann et al. (2009) also found dynamic photoinhibition during the day in different oak species indicating that the light-harvesting capacity exceeded both, the capacity to utilize energy through photosynthesis and the ability of heat dissipation. A photoinhibition effect may also explain the depression of $P_{\text{max}}$ quite early in the day at the beginning of the growing season (Fig. 5A), due to high morning irradiance, as similarly reported by Yang et al. (2004). Consistently, in spring, Siam et al. (2008) observed an early depression of $P_{\text{max}}$, around 10 h, mostly in Q. pubescens and less so in Q. frainetto.

In mid-summer, high air temperatures led to stomatal closure-induced midday depression of photosynthesis of both oaks (Figs. 1, 5B). This response was more intense in OLY, probably due to the almost absence of rainfall in mid-summer (Fig. 1), ensuring a higher WUE of the seedlings in OLY than in SWA (Fig. 4SH, supplement). Epron et al. (1992) and Peña-Rojas et al. (2004) reported that depression of $\varphi_P$ can facilitate the protection of PSII due to increasing thermal energy dissipation, so that summer drought does not cause permanent photodamage to the photosynthetic apparatus. However, in our study, only a mild reduction of $\varphi_P$ and recovery to approximately 0.8 was observed in both species in the mid-growing season (Fig. 3B).

**Differences between oak species and provenances under contrasting growth regimes:** The two replicate common gardens were characterized by differences in growth conditions; OLY was drier and established under high light intensity, whereas SWA had higher precipitation and lower radiation due to the northern latitude in addition to the effect of adult trees’ canopies. The deviation in growth conditions, particularly solar radiation and VPD, among the two common gardens is also indicated by PCA analysis (Fig. 2S, supplement). This enabled the assessment of the performance of the two oaks and provenances to a changing environment and their evaluation for assisting migration purposes.

These differential regimes affected PSII efficiency and resulted in lower chlorophyll $a$ fluorescence values in the southern vs. the northern common garden (Fig. 2A, D), attributed to an efficient strategy for light acclimation (Adams and Demmig-Adams 2004, Pollastrini et al. 2016) in the former and the favorable effect of partial shading (Flores and Jurado 2003, Valladares et al. 2008, Caldeira et al. 2014, Martin-Alcón et al. 2016) which reduces leaf temperatures, water evaporative demand, and photoinhibition in the latter. By disassembling the predawn values of $P_{\text{max}}$ into its components, not only $\varphi_P$ but also RC/ABS and $\psi_E$ were enhanced (Fig. 1S) in the SWA common garden, consistent with the results of Bantis et al. (2020). Interestingly, solely the plants in SWA showed a significant decrease of $\varphi_P$, predawn values (Fig. 1SG) from the beginning to the mid-stage of the growing season. This has been observed for different species of the Mediterranean maquis vegetation where new, fully developed leaves showed the highest predawn $\varphi_P$ values, whereas older leaves in the summer season showed a depression (Werner et al. 2002) but could not be confirmed for the plants in OLY where values tended to show higher values in the mid-stage of the growing season (Fig. 1SH).

Overall, in SWA, Q. pubescens showed higher $P_{\text{max}}$ values, compared to Q. frainetto, following previous studies (Holland et al. 2014, Koller et al. 2020, Bantis et al. 2021). Striking is a strongly significant increase in predawn $P_{\text{max}}$ values of Q. pubescens in SWA at the end of the growing season (Fig. 1SA), due to increased $\psi_E$, the probability that an absorbed photon leads to a reduction further than $Q_0$, which could not be observed in Q. frainetto (Fig. 1SE). This could explain the greater height of Q. pubescens compared to Q. frainetto in SWA (Bantis et al. 2021). Due to a better performance in the late phase of the vegetation period and an overall longer vegetation period of the species (Holland et al. 2014), biomass production can be increased enormously under good climatic conditions. In contrast, assimilation rates during the day did not differ between sites (Fig. 4A) or between species (Fig. 4B), even during the last phase of the growing period (Fig. 5C). Valladares et al. (2005) also concluded that photoinhibition under high light intensity and drought had a minor effect on the performance of Mediterranean woody seedlings and estimated that plant carbon gain was reduced only by 3%. Probably, the protection of PSII, as indicated by the lower $P_{\text{max}}$ and $\varphi_P$ in OLY, also supported the sufficient functioning of the photosynthetic apparatus, as already shown in drought-stressed sessile oaks in Northeast France (Epron et al. 1992) and water-depleted holm oak seedlings (Peña-Rojas et al. 2004). Thus, the seedlings adapted to repetitive stressful summer conditions in south Mediterranean conditions managed to be equally productive, in terms of $CO_2$ assimilation, with those growing under a more favorable growth regime in Germany.

The considerably different growth conditions of the two common gardens were not reflected in the respective differences between the studied species. Q. pubescens, compared to Q. frainetto, presented only a slightly
higher maximum quantum yield of PSII than Q. frainetto (Figs. 2B, 3A–C) and a smaller midday depression of PLPSII (Fig. 2E) which was, however, not evident throughout the growing season (Fig. 3D–F). Still, the slightly enhanced chlorophyll a fluorescence traits of Q. pubescens was not related to improved PNmax or other gas-exchange diurnal patterns, compared to Q. frainetto, except for the higher water-use efficiency of the former in mid-summer (Fig. 5). Consistently, Pollastrini et al. (2020) reported similar g levels in the two oaks. Thus, our hypothesis that Q. pubescens would outperform Q. frainetto, as reported by several studies on the two species’ chlorophyll fluorescence and gas-exchange responses, as well as water balance and growth (e.g., Fotelli et al. 2000, Siam et al. 2009, Bantis et al. 2019, 2021; Pollastrini et al. 2020) was only partially verified by our findings. Similarly, we detected no clear differences between the studied oak provenances. Better performance of the Greek detected no clear differences between the studied oak provenances was only partially verified by our findings. Similarly, we assimilation of nonstressed oak species native to higher latitudes was higher than the studied Mediterranean oaks in the German common garden. However, the oaks in SWA were not watered and depended solely on precipitation for their water supply, whereas they were also experiencing the exceptionally warm summer of 2019 in Germany. Thus, their competitive potential, in terms of assimilation, seems quite advanced particularly compared to the above-mentioned drought-stressed Q. robur and Q. petraea. Still, these observations should be treated with caution, given the differences between the recorded assimilation parameters (PNmax or PSII) and between the measuring conditions.

Conclusion: By 2100, it is anticipated that oaks will be a highly important genus for more than 30% of forests in Europe (Hanewinkel et al. 2013) to cope with the ongoing warming and the increase in frequency and intensity of heat and drought events. Forest management initiatives such as assisted migration may be necessary to compensate for the long regeneration time of forest ecosystems. Our results indicate that, from their photosynthetic performance under field conditions, the Mediterranean species Q. frainetto and Q. pubescens are both suitable for planting in Central Europe, especially because the growing season of 2019 was equally warm in Germany as in Greece. Although both species exhibited an overall high photosynthetic efficiency, Q. pubescens presented more advantageous chlorophyll a fluorescence traits at the late stage of the growing season. The beneficial effects of sheltering on the survival and photosynthetic efficiency of planted oaks could be taken into consideration for future assisted migration schemes. If xerothermic conditions in central Europe are to become as intense as in the eastern Mediterranean, and the survival of planted oak seedlings declines, still the best-adapted individuals appear to be able to develop photoprotective and drought-protective mechanisms to sustain their survival and growth. Since only negligible differences were found between provenances, it should be considered whether enlarging the gene pools of Q. pubescens and Q. frainetto by introducing more provenances would increase the occurrence of planting material with enhanced inherent tolerance to adverse climatic conditions.

References

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