



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

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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 *a* 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 *a* 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-

Highlights

- High radiation led to strong photoinhibition of both oaks at the southern site
- At both sites, only small differences were observed between species and provenances
- Both oak species show high potential for assisted migration to Central Europe

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Abbreviations: DOY – day of the year; g_s – stomatal conductance; OLY – Olympiada/Greece; PI_{abs} – performance index on absorption basis; P_{Nmax} – light-saturated net photosynthetic rate; RC/ABS – active reaction centers on absorption base; SWA – Schwanheim/Germany; WUE – water-use efficiency; $\Phi P_0 - F_v/F_m$ – maximum quantum efficiency of the reduction of Q_A ; ΨE_0 – the probability that an absorbed photon leads to a reduction further than Q_A .

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Guldberg *et al.* 2018, Spinoni *et al.* 2018). Based on the anticipated altitudinal and latitudinal shift of climate zones from the equator poleward (Loarie *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., Bréda *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 (Valladares *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 (Früchtenicht *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 oaks 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.), and Olympiada, 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_{Nmax}) and stomatal conductance (g_s) 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-cm² cuvette and the cuvette was firmly closed to ensure stable measurements. Photosynthetically active radiation (PAR) was set at 1,000 $\mu\text{mol}(\text{photon})\text{m}^{-2}\text{s}^{-1}$, 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 CO₂ flow rate in the chamber was set to 300 $\mu\text{mol s}^{-1}$, reference CO₂ 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_{Nmax} to g_s .

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_0 according to Strasser *et al.* (2000, 2004). Although recent studies showed a better fitting of earlier F_0 values to extrapolated 'true' F_0 (e.g., 20 μs ; Padhi *et al.* 2021), we chose to use 50 μs as F_0 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: ϕP_0 (F_v/F_m) and the performance index on an absorption basis [$PI_{abs} \equiv 10 RC/ABS \phi P_0 / (1 - \phi P_0) \psi E_0 / (1 - \psi E_0)$] 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_{abs} (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, ϕP_0 and PI_{abs} 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 (ϕP_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 ϕP_0 , compared to

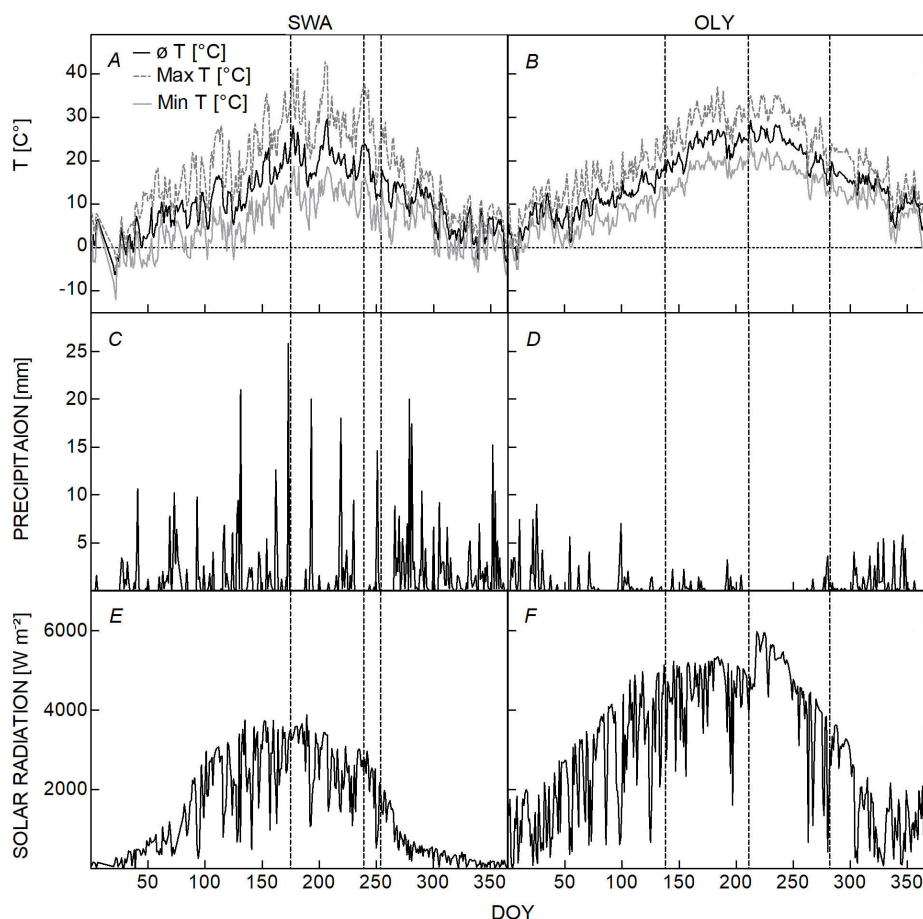


Fig. 1. Air temperature [$^{\circ}\text{C}$] (A,B), daily sum of precipitation [mm] (C,D), and daily sum of solar radiation [W m^{-2}] (E,F) of SWA – Germany (left) and OLY – Greece (right) in 2019. Daily minimum (grey line) and maximum (dashed line) air temperatures are indicated on the scale above 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.

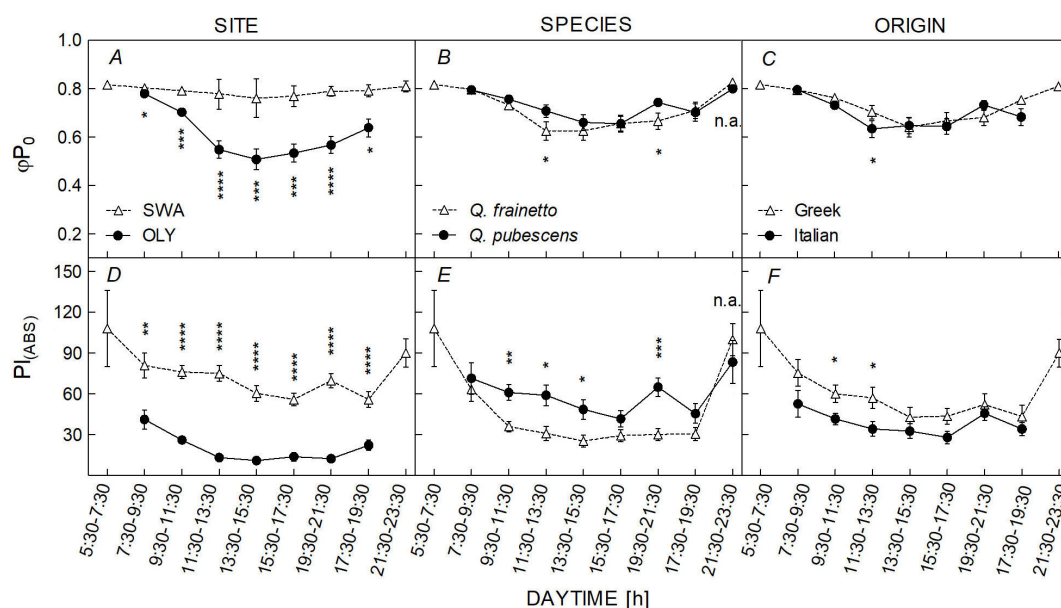


Fig. 2. Diurnal course of the maximum quantum efficiency of reduction of Q_A (ϕP_0) and the performance index on absorption basis (PI_{abs}) shown as mean values \pm SE. Data are grouped and compared site-wise (A,D) SWA/OLY; $n = 2-45$, species-wise (B,E) *Q. frainetto*/*Q. pubescens*; $n = 2-48$, and provenance-wise (C,F) Italian/Greek; $n = 2-47$. 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.

Q. frainetto only twice during the day (Fig. 2B). Consistent with ϕP_0 , PI_{abs} values were on average 48 ± 10 units higher in the German than those in the Greek common garden (Fig. 2D). *Q. pubescens* showed significantly higher PI_{abs} than *Q. frainetto* almost throughout the day, except at the beginning and the end of the measurements. The differences between the provenances were less pronounced, as PI_{abs} 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 ϕP_0 and PI_{abs} 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 PI_{abs} 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 (PI_{abs} , ϕP_0 ; $p < 0.0001$) between the two common gardens. On both sites, the PI_{abs} 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_0 values. In SWA, ϕP_0 values decreased significantly in *Q. frainetto* from the early to the mid-stage of the growing season. In *Q. pubescens*, ψE_0 and PI_{abs} increased significantly from the early to the late stage of the growing season. In OLY, except ϕP_0 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 P_{Nmax} , g_s , 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 P_{Nmax} and g_s 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. P_{Nmax} was significantly higher at OLY vs. SWA only early in the morning and between 13:30 h and 15:30 h (Fig. 4A), whereas no significant differences in g_s 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 P_{Nmax} and g_s 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 P_{Nmax} and g_s 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 P_{Nmax} and g_s 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 P_{Nmax} values early in the day, in the middle of the growing season (Fig. 5A–C). Despite its decrease in autumn, a considerable P_{Nmax} was still measured in autumn (Fig. 5C). Then, the greatest g_s values were recorded (Fig. 5F). Regardless of these seasonal fluctuations, no clear differences were detected

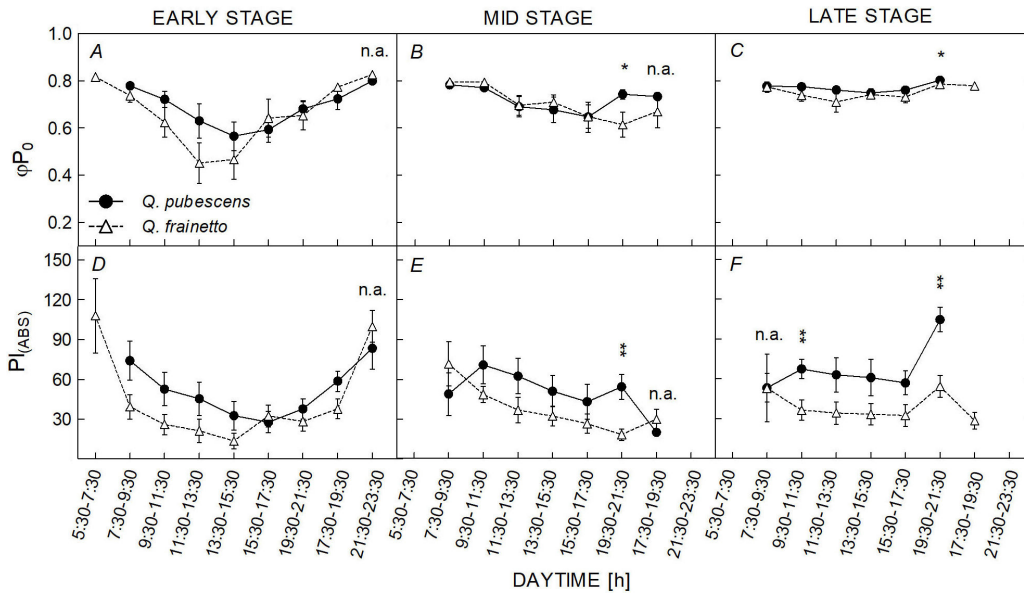


Fig. 3. Diurnal course of the maximum quantum efficiency of reduction of Q_A (ϕP_0) (A–C) and the performance index on an absorption basis (PI_{abs}) (D–F), measured at three dates per species (early, mid, and late stage of the growing season) shown as mean values \pm SE ($n = 2-21$). Statistically significant 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.

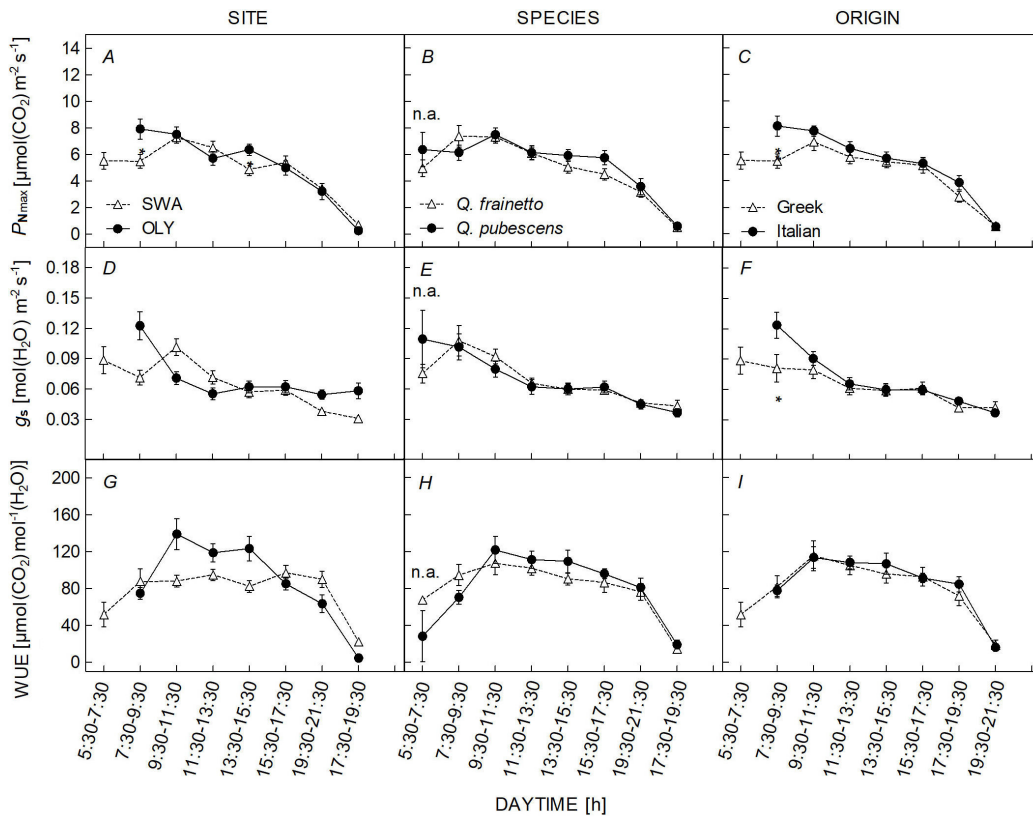


Fig. 4. Diurnal course of light-saturated net photosynthetic rate (P_{Nmax}), stomatal conductance (g_s), and water-use efficiency (WUE), shown as mean values \pm SE. Data are grouped and compared site-wise (A,D,G) SWA/OLY; $n = 5-43$, species-wise (B,E,H) *Q. frainetto*/*Q. pubescens*; $n = 2-43$, and 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.

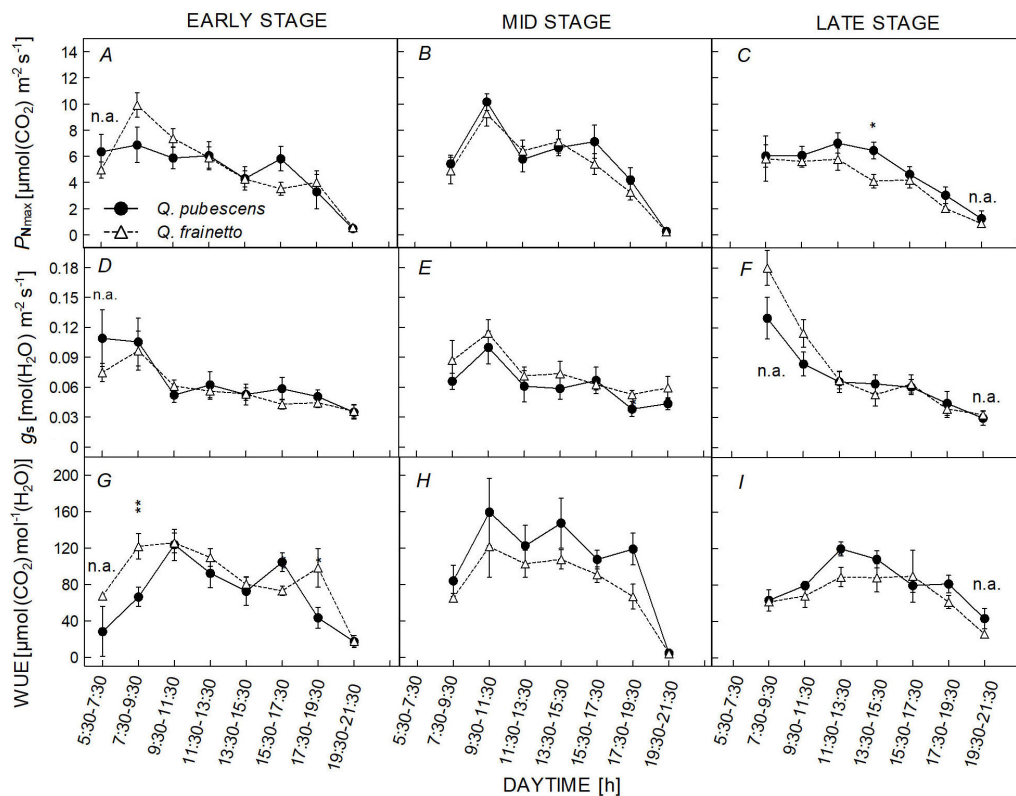


Fig. 5. Diurnal course of light-saturated net photosynthetic rate (P_{Nmax}) (A–C), stomatal conductance (g_s) (D–F), and water-use efficiency (WUE) (G–I), measured at three dates per species (early, mid, and late stages of the growing season) shown as mean values \pm SE ($n = 1–17$). Statistically significant 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.

between the two oak species. *Q. pubescens* vs. *Q. frainetto* tended to exhibit higher P_{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 ϕP_0 and PI_{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 ϕP_0 reflects only the maximum quantum yield of (mainly) PSII

primary photochemistry ($F_v/F_m = \phi P_0$; Strasser *et al.* 2000, 2004) and is widely used to estimate the degree of photoinhibition (Tezara *et al.* 2005), the PI_{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 ϕP_0 : RC/ABS reflecting the active reaction centers on absorption base, and ψE_0 , expressing the probability that an absorbed photon leads to a reduction further than Q_A (Strasser *et al.* 2000, 2004). Additionally, PI_{abs} vs. ϕP_0 , is more sensitive to various stressors, such as decreasing leaf water content, and is therefore often used as a general fitness parameter (Jedrowski *et al.* 2014, 2015).

Midday depression and seasonal variability: A clear depression of ϕP_0 and PI_{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 PI_{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

et al. 1989, Zhang and Gao 1999, Zhang *et al.* 2001) also including evergreen Mediterranean oaks (Baquedano and Castillo 2007).

A midday depression, although less intense, was also detected in both oaks for P_{Nmax} and g_s , 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 ϕP_0 and PI_{abs} 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.* 1995) 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_{Nmax} 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_{Nmax} , 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 ϕP_0 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 ϕP_0 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, Martín-Alcón *et al.* 2016) which reduces leaf temperatures, water evaporative demand, and photoinhibition in the latter. By disassembling the predawn values of PI_{abs} into its components, not only ϕP_0 but also RC/ABS and ψE_0 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 ϕP_0 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 ϕP_0 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 PI_{abs} 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 PI_{abs} values of *Q. pubescens* in SWA at the end of the growing season (Fig. 1SA), due to increased ψE_0 , the probability that an absorbed photon leads to a reduction further than Q_A , 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 PI_{abs} and ϕP_0 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 PI_{abs} (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 P_{Nmax} 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_s 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 vs. the Italian provenance, in line with Bantis *et al.* (2020), was observed only in terms of PI_{abs} (Fig. 2F), among all tested parameters. The slightly more advantageous performance of local provenances can be attributed to their long-term adaptation to local environmental conditions (Boshier *et al.* 2015). In the same context, Pollastrini *et al.* (2020), assessed photosynthesis and chlorophyll *a* fluorescence in the common garden in Sant'Anatolia di Narco, Italy, and reported that the local Italian provenances outperformed the Greek one there. Bantis *et al.* (2021) also concluded that only small, site-specific, differences between the two provenances were observed when their performance was compared in the three replicate common gardens in Germany, Greece, and Italy. Thus, our second hypothesis about the differential performance of the two oak provenances in the two common gardens is not supported.

Q. robur L. and *Q. petraea* (Matt.) Liebl. are predominant in Central and Northern Europe and are believed to contribute to European forests' adaptation to climate change (Schroeder *et al.* 2021). A comparison of the photosynthetic efficiency of *Q. pubescens* and *Q. frainetto* with that of such oaks could provide some indication of the potential competitive performance of the studied Mediterranean oaks outside their natural distribution range. In the absence of drought stress, Morecroft and Roberts (1999) and Morecroft *et al.* (2003) found the highest P_{Nmax} of ca. 10.5 to 18 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in *Q. robur* in southern England, whereas P_{Nmax} within this range was also recorded by Both and Brüggemann (2009) in central Germany. Similarly, the highest net photosynthetic rates (P_N) measured by Epron *et al.* (1992) and Epron and Dreyer (1993) were ca. 14–18 and 15 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in watered *Q. robur* and *Q. petraea* trees, respectively, in northern France. However, in the same studies, P_N of drought-stressed trees, particularly in mid-summer, decreased to lower than 5 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in both oaks. Thus, the 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 (P_{Nmax} or P_N) 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.

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