

Recovery of water potential and leaf gas exchange performance following drought stress in *Quercus cerris* populations

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Drought and global warming are major environmental stressors that significantly affect forest ecosystems and the survival of tree species. This study investigates the physiological and biochemical responses of Turkey oak (*Quercus cerris* L.) seedlings from five populations across three bioclimatic zones in Turkey – semi-arid (Yozgat), semi-humid (Isparta, Balıkesir), and humid (Çanakkale and Sinop) – to drought stress and subsequent re-watering. Seedlings were subjected to control (regular irrigation) and drought stress (no irrigation for 30 days), with ecophysiological (soil water content, midday water potential, gas exchange) and biochemical (total soluble sugars and chlorophyll content) traits measured on days 10, 20, 30, and after re-watering (days R3 and R10). Drought stress reduced midday water potential and gas exchange parameters across all populations. Total soluble sugar content increased under drought, except in the Sinop population, which showed a decline in photosynthetic rate and failed to accumulate soluble sugars. In contrast, the Yozgat population maintained higher midday water potential, suggesting effective osmotic regulation. Other populations (Isparta, Balıkesir, and Çanakkale) coped with drought by increasing total soluble sugar content despite lower water potential. Following re-watering, water potential and sugar content recovered in all populations, with a gradual improvement in photosynthetic performance. These findings highlight significant intraspecific variation in drought response among *Q. cerris* populations and underscore the importance of considering population-level differences in forest management and afforestation strategies under changing climate conditions.

Keywords: Drought, Gas Exchange, Recovery, Soluble Sugar, *Quercus* Populations

Introduction

Climate is one of the most critical factors shaping life on Earth and determining the distribution of organisms across ecosystems (Bulut & Gürkan 2017). Global climate variability has a major impact on forests (Lempereur et al. 2015, Nunes et al. 2021). Among these factors, global warming is a key driver of environmental change, directly impacting plant species' survival, growth, and overall performance. As climate change intensifies, a better understanding of the functional traits of tree

species, particularly those related to drought tolerance, is crucial for predicting ecosystem responses (De la Riva et al. 2018).

Woody species show considerable variation in their ability to cope with drought, particularly in regions facing prolonged aridity (Alon et al. 2023). Extensive research has been conducted on plant responses to drought stress, which occur at morphological, physiological, and molecular levels across various forest species (Zhang et al. 2004, Deligöz & Bayar 2018, Jafarnia et al. 2018). Trees adapt to water stress through changes in growth, gas exchange, and water relations, with stomatal closure being a key indicator of plant water stress (Grant et al. 2010, San-Eufrasio et al. 2020). Drought leads to reduced growth and photosynthesis (Flexas et al. 2004, Farooq et al. 2009), lower stomatal conductance (Deligöz & Bayar 2018), reduced hydraulic conductance (Rzigui et al. 2018), and altered nonstructural carbohydrate dynamics (McDowell 2011).

A comprehensive understanding of geographic patterns and genetic variation in functional and structural traits of key tree species is critical for informing adaptive forest management strategies to mitigate the projected impacts of climate change on

plant growth and drought tolerance (Cocozza et al. 2016). In this context, provenance trials are valuable tools for assessing individual trees' capacity to adapt to varying environmental conditions (Stojnić et al. 2015).

The genus *Quercus*, comprising nearly 600 species worldwide, includes both trees and shrubs that occupy a wide range of habitats, from temperate to subtropical forests and from humid to extremely dry environments (Nixon 2006) and form forests of high cultural, ecological, and commercial value (Sobrino-Plata et al. 2023). In Turkey, oak species cover a significant area, with approximately 6.92 million hectares of forest, representing a substantial part of the country's forest ecosystem (GDF 2022). Genetic variation plays a key role in the observed differences in drought tolerance within and among *Quercus* species (Dickson & Tomlinson 1996, Arend et al. 2011, Fririon et al. 2023, Atar et al. 2024). Among these species, *Quercus cerris*, commonly known as the Turkey oak, has shown particular promise in the context of climate change, especially in Central and Western Europe, due to its notable drought tolerance. This species offers substantial potential for adaptive forestry practices owing to its distinct evolutionary history, drought-re-

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sistant strategies, and high phenotypic and genetic variability (Lados et al. 2024).

In Mediterranean regions, where oaks experience prolonged summer droughts, evergreen and deciduous species exhibit distinct drought-response strategies. Evergreen oaks, such as *Quercus ilex* L., often recover more quickly from dry periods by resuming growth after drought stress (Campelo et al. 2023). Manes et al. (2006) found that during drought, *Q. ilex* maintains root growth and keeps its stomata open, while the deciduous *Q. cerris* exhibits higher photosynthetic capacity under water-abundant conditions. Moreover, even among deciduous oaks, drought tolerance varies; for instance, *Q. cerris* is more drought-tolerant than *Q. pubescens* (Tognetti et al. 2007). The ability of species such as *Q. cerris* to maintain water uptake as soil moisture declines is vital to their success in increasingly arid climates (Köcher et al. 2009).

A thorough understanding of how tree populations respond to drought is particularly important, as it is essential for predicting species adaptability to climate change and for guiding afforestation efforts in vulnerable Mediterranean ecosystems. Although interest in *Q. cerris* and other Mediterranean oaks is growing, studies comparing early drought responses across populations from different bioclimatic zones remain limited. Despite *Quercus cerris* is recognized for its drought tolerance, population-level variation in physiological and biochemical responses to water deficit remains insufficiently characterized.

By examining multiple populations from contrasting bioclimatic zones, we explore intraspecific variation in drought tolerance, a topic for which limited data exist for this species. This study investigates drought-induced changes in midday water potential, gas exchange, and osmotic regulation in three-month-old seedlings from five *Q. cerris* populations originating from contrasting bioclimatic zones in Turkey. We hypothesize that seedlings from semi-arid regions exhibit greater drought tolerance than those from more humid climates, as reflected in their ecophysiological and biochemical traits. By integrating climate-origin information with drought-response metrics across multiple populations, this study provides a population-level framework for

identifying adaptive traits relevant to future seed transfer, provenance selection, and breeding programs under increased drought frequency. Identifying populations better suited to cope with future droughts will enhance the sustainability and productivity of Mediterranean forest ecosystems under climate change.

Material and methods

Plant material and climate data

Seed material was obtained from five populations of Turkey oak trees (Yozgat, Balıkesir, Isparta, Çanakkale, Sinop – see Fig. S1 in Supplementary material) representing three different bioclimate zones (semi-arid, semi-humid, and humid) based on Emberger’s bioclimate categories (Akman 2011). In October 2021, seeds were collected from at least 10 trees per population and stored in polyethylene bags at +4 °C. At the beginning of March 2022, the seeds were planted in polyethylene tubes (11.0 cm in diameter × 22.0 cm in height) with a humus-perlite mixture (3:1, v/v). Climate data were gathered from the WorldClim database, which provides worldwide climate data as spatial data layers (Fick & Hijmans 2017). Based on Emberger’s bioclimatic classification, the five populations belong to three bioclimate classes: semi-arid, low-humid, and humid (Tab. 1).

Experimental design and stress application

All seeds had germinated by the start of the experiment, and seedlings with uniform height and diameter were used. Seedlings were regularly irrigated in the greenhouse, and routine maintenance (e.g., cleaning and weeding) was performed. Three-month-old oak seedlings were then subjected to two water treatments (control and drought), with three replicates each, according to Emberger’s bioclimate classification. We used a randomized trial design, with 2 water treatments [irrigation (control) and no irrigation (drought stress)] × 5 populations × 3 replicates × 30 seedlings per replicate, totaling 900 seedlings. As for the first treatment (control), seedlings were kept under well-watered conditions throughout the experimental period, i.e., they were watered to field capacity every 2 or 3 days. In the sec-

ond treatment, seedlings were subjected to water-deficit stress by withholding water for 30 days. On the 10th, 20th, and 30th days, measurements were taken in the greenhouse. The seedlings were irrigated to field capacity (recovery) on the 30th day, and physiological and biochemical properties were measured on the 3rd and 10th days after rewatering (see also Fig. S2 in Supplementary material). To facilitate the presentation of the results, measurements taken 3 days after rewatering are shown as “R3”, and those taken on the 10th day after rewatering are shown as “R10”. Accordingly, results are displayed in diagrams using the labels 10, 20, 30, R3, and R10 (Fig. S2).

The temperature and relative humidity in the greenhouse were measured using a datalogger since the beginning of the experiment. During the experiment, the average air temperature ranged from 15.8 to 28.9 °C, and relative humidity from 23.3% to 65.3%. On the measurement days (10, 20, 30, R3 and R10), the average air temperature ranged from 21.4 to 25.5 °C, while the average air humidity ranged from 35.7% to 58.65%.

Ecophysiological traits

Physiological traits (midday water potential, net photosynthetic rate, stomatal conductance, and transpiration rate) and biochemical traits (total soluble sugar and chlorophyll content) of seedlings from the five populations of *Q. cerris* were measured in a greenhouse during July and August 2022, and subjected to drought stress followed by rewatering.

Midday water potential (Ψ_{md}) and soil water content (SWC)

A Scholander pressure chamber (Model 600, PMS Instruments, Corvallis, OR, USA) was used to measure the leaf water potential (Ψ_{md} , Mpa – Scholander et al. 1965). Shoot samples were randomly collected from the six seedlings in each group (control and drought stress) and measured between 12:00 and 13:00 pm. At the same time, soil volumetric content was measured with 5 replications on the same seedlings used for physiological measurements by the probe TDR 300 (Fieldscout, Portland, OR, USA) in the top 12.5 cm of soil.

Gas exchange measurements

Gas exchange parameters were determined on mature leaves in the greenhouse using a portable photosynthetic equipment model LI-6400XT (LiCOR, Lincoln, NE, USA), in three replicates. Between 08:30 and 11:30 and 13:30 and 15:00, all measurements were carried out using a 6 cm² chamber and a linked light source (6400-02B-red/blue/light). The manufacturer’s recommended calibration procedure was followed. A reference CO₂ level of 400 ppm, an air flow rate of 500 $\mu\text{mol s}^{-1}$, and photosynthetic active radiation (PPFD) of 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ were maintained. During the measurement, the leaves’ temperature

Tab. 1 - Coordinate and climate data and bioclimatic types of *Q. cerris* populations. (S): summer drought index value; (Q): precipitation-temperature coefficient; (Med.): Mediterranean.

Population	Latitude N	Longitude E	Altitude (m)	S	Q	Bioclimatic type	
						S	Q
Yozgat	39° 59' 05"	35° 13' 42"	1304	2.5	53.4	Med.	Semi-arid
Balıkesir	39° 27' 31"	28° 29' 52"	1010	2.7	94.3	Med.	Semi-humid
Isparta	37° 39' 31"	31° 12' 14"	1400	2.6	69.3	Med.	Semi-humid
Çanakkale	39° 42' 33"	26° 44' 52"	988	2.5	104.1	Med.	Humid
Sinop	41° 52' 34"	34° 54' 15"	305	4.8	103.5	Med.	Humid

was adjusted to match the ambient temperature. The net photosynthetic rate ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), stomatal conductance ($\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$), transpiration rate ($\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$), and intercellular CO_2 concentration ($\mu\text{mol mol}^{-1}$) were determined.

Total soluble sugar (TSC)

For total soluble sugar analysis, leaf samples were collected from seedlings on the 10th, 20th, and 30th day of treatment, as well as 3rd and 10th days after rewatering. Leaf samples were taken from the same seedlings used for physiological measurements. An average of 6 seedlings (all leaves) for each sampling day in each treatment were analyzed. After cleaning in distilled water, leaves were dried at 65 °C for 48 hours and then ground using a coffee grinder. For each sample, 100 mg of ground sample were incubated, and total soluble sugar content ($\text{mg g}^{-1} \text{ DW}$) was determined according to Dubois et al. (1956).

Leaf chlorophyll content (Chl)

Chlorophyll concentration was determined using four replicates of leaves from each treatment using the portable device SPAD-502 Plus (Konica Minolta, Inc., Osaka, Japan). It was measured three times by cleaning the leaf surface on one leaf (tip, middle, and near the petiole), and the average value was calculated.

Data analysis

A two-way analysis of variance (ANOVA) was used to examine the biochemical and physiological data, with “population” and “drought stress” acting as the constant factors. Sampling time served as the within-subjects factor, and “population” and “drought stress” as the main between-subjects factors. Changes in leaf gas exchange metrics during the investigation were tested. The relationship between factors, physiological and biochemical characteristics of seedlings was also assessed using principal component analysis (PCA).

Results

Water potential and soil water content

On day 30, the volumetric soil water content of drought-stressed seedlings ranged from 1.6% to 2.3%, while the populations’ midday water potential ranged from -3.5 to -4.5 MPa. *Quercus cerris* seedlings subjected to drought treatment on days 10, 20, and 30, followed by re-watering, showed significant changes in midday water potential and volumetric soil water content between treatments (Fig. 1, Fig. 2). Three days after re-irrigation, a significant difference in volumetric soil water content was observed between control and drought-stressed seedlings. Additionally, there was a significant positive correlation ($R^2 = 0.783, P < 0.01$) between soil water content

and midday water potential. As soil water content decreased, the midday water potential also decreased significantly. Volumetric soil water content was restored by day 10 after re-watering (Fig. 1).

Regarding midday water potential, interactions across populations, treatments, and sampling times were highly significant ($P < 0.01$ – Tab. 2). Midday water potential decreased gradually with increasing drought stress. In the semi-arid Yozgat population, the highest midday water potential (-3.5 MPa) was found on the 30th day of drought stress. The lowest midday water potential (-4.5 MPa) was recorded in the Çanakkale population, originating from a humid climate. Midday water potential of previously stressed plants reached levels comparable to those of control plants by the end of the drought-recovery phase (R3 – Fig. 2). On the third day of recovery following drought stress, midday water potential was similar across all treatments.

Photosynthetic traits at the leaf level

Drought stress was followed by a progressive decrease in net photosynthetic rate (*Anet*), stomatal conductance (*gs*), and transpiration (*E*) in all populations (Fig. 3a-b, Fig. 4a). The rate of decline in gas exchange parameters varied among populations. The interactions between the sampling time, populations and treatments for these variables (sampling time × popula-

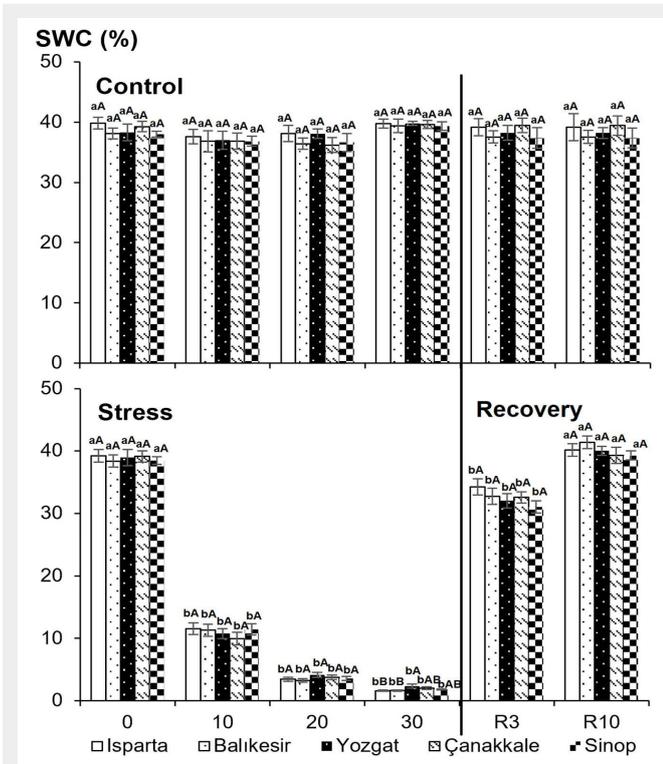


Fig. 1 - Effects of drought stress on volumetric soil water content in five *Q. cerris* populations subjected to different drought treatments. Data are presented as means ± standard error (SE). Differences between treatments are shown with lower-case letters, while differences between populations are indicated with upper-case letters.

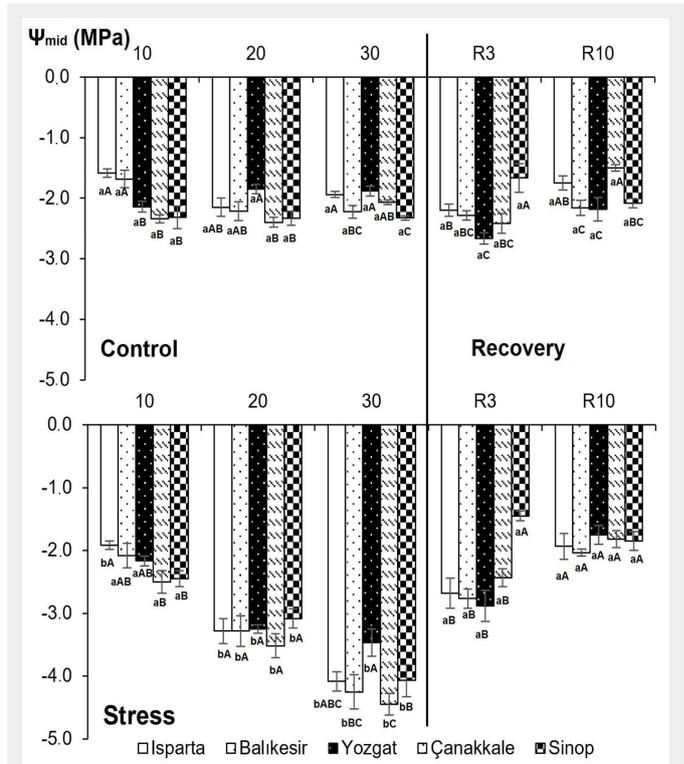


Fig. 2 - Effects of drought stress on midday water potential in five *Q. cerris* populations subjected to different drought treatments. Data are presented as means ± standard error (SE). Differences between treatments are shown with lower-case letters, while differences between populations are indicated with upper-case letters.

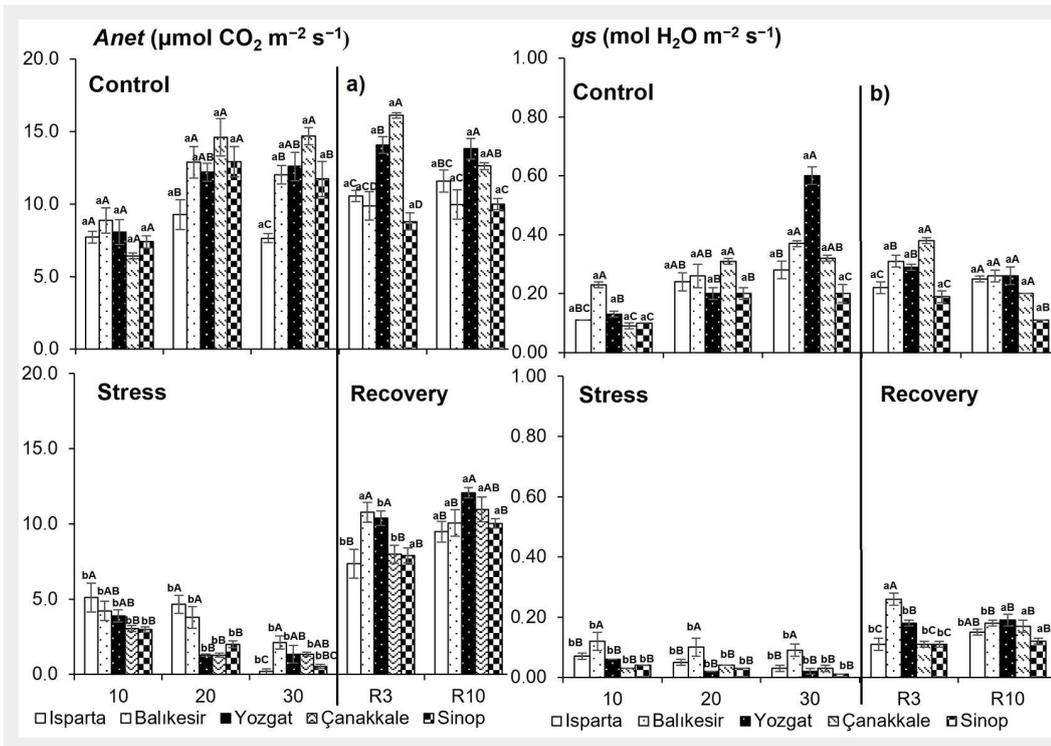


Fig. 3 - Photosynthetic characteristics (a: net photosynthetic rate, Anet; b: stomatal conductance, gs) of *Q. cerris* seedlings grown under the different drought treatments. Data are presented as means \pm standard error (SE). Differences between treatments are shown with lower-case letters, while differences between populations are indicated with upper-case letters.

tion, population \times drought stress and sampling time \times drought stress interaction, $P < 0.01$) were also highly significant (Tab. 2). During the drought-recovery period (days 3-10), previously stressed plants began to increase Anet, gs, and E in some populations by day 3 and in others by day 10 after re-watering. By the end of the recovery period, Anet generally reached levels comparable to those of control seedlings. Intercellular CO_2 concentrations differed significantly between treatments in all popula-

tions on the 30th day of drought stress. Accordingly, drought-stressed seedlings had higher intercellular CO_2 concentrations (Fig. 4b). No significant differences in intercellular CO_2 concentration were observed between treatments on the 10th day after re-watering.

The results of the principal component analysis are summarized in Fig. S3 (Supplementary material). According to the PCA, the highest Pearson's correlation coefficient (r) with PC1 (variance accounted for:

67.4%) was recorded for ψ_{mid} ($r=0.864$), SWC ($r=0.920$), Anet ($r=0.915$), gs ($r=0.862$), E ($r=0.925$), TSC ($r=0.621$), and Chl ($r=0.843$). Midday water potential was positively correlated with volumetric water content, net photosynthetic rate, stomatal conductance, transpiration rate, and chlorophyll pigment content, and negatively correlated with intercellular CO_2 concentration and total soluble sugar content.

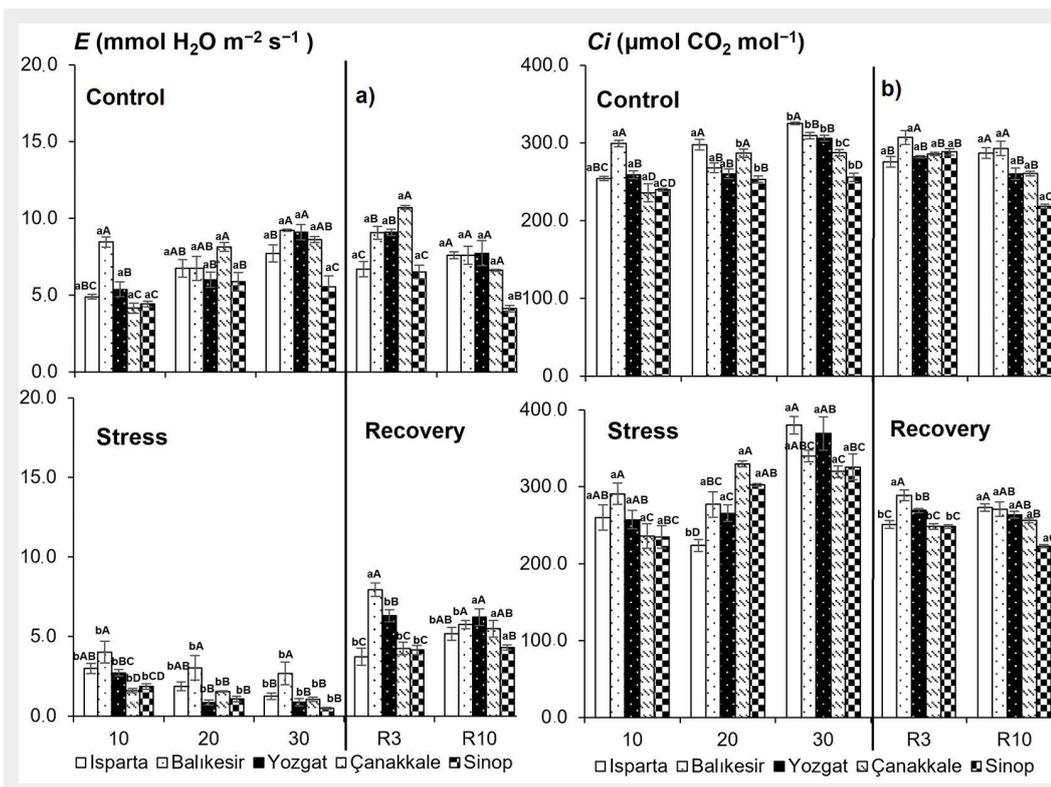


Fig. 4 - Impact of drought stress on (a) transpiration rate (E) and (b) intercellular CO_2 concentration (C_i) under different drought treatments. Data are presented as means \pm standard error (SE). Differences between treatments are shown with lower-case letters, while differences between populations are indicated with upper-case letters.

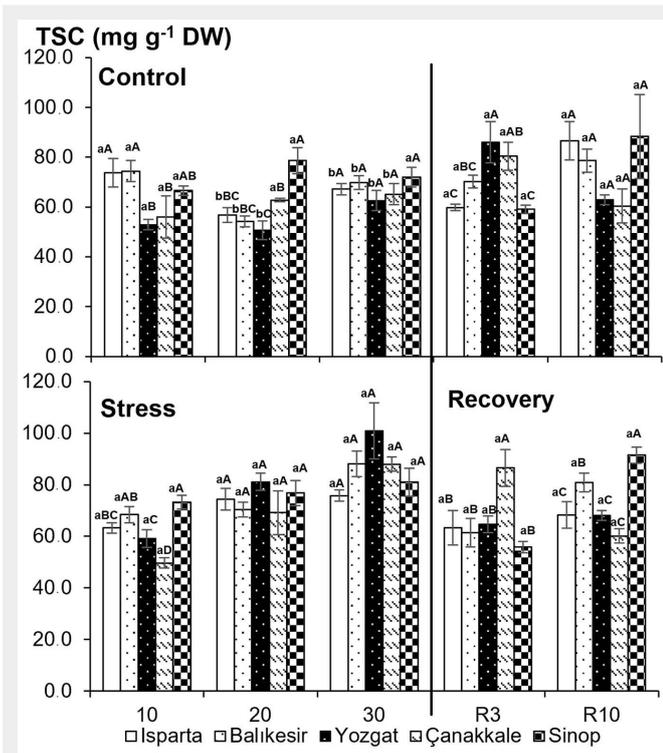


Fig. 5 - Total soluble sugar (TSC) content in five *Quercus cerris* populations under control and drought stress conditions. Data are presented as means \pm standard error (SE). Differences between treatments are shown with lower-case letters, while differences between populations are indicated with upper-case letters.

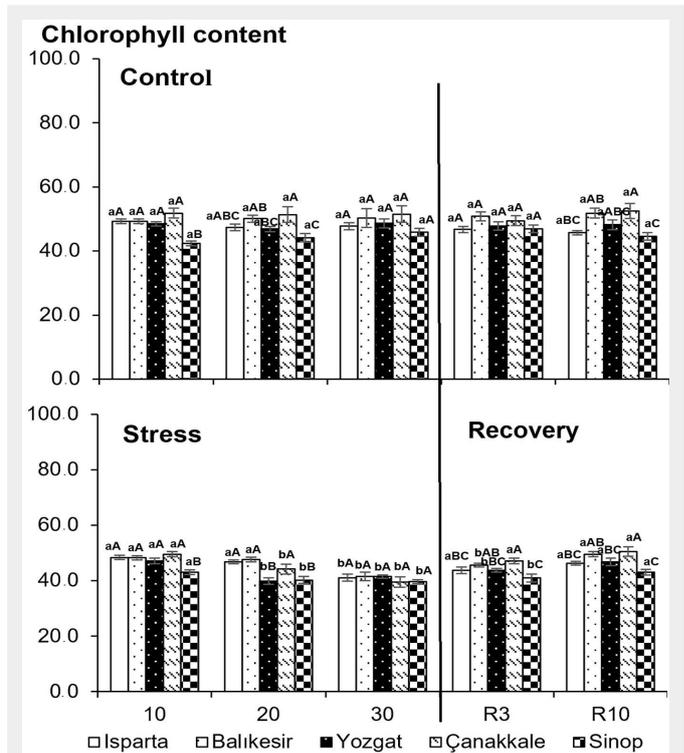


Fig. 6 - Effects of drought stress on chlorophyll content in five *Q. cerris* populations grown under different drought treatments. Data are presented as means \pm standard error (SE). Differences between treatments are shown with lower-case letters, while differences between populations are indicated with upper-case letters.

Biochemical traits in response to drought

Examining the effects of sampling time and drought stress on total soluble sugar by ANOVA revealed significant main effects of time and drought stress, as well as the time \times drought stress interaction ($P < 0.01$ – Tab. 2). Total soluble sugar content increased with drought stress. Differences were significant among treatments, except for the Sinop population on day 30. On day 3 of re-watering, the total soluble sugar content in the drought-stressed treatments was close to that of the control treatment across all populations (Fig. 5). The total soluble sugar content recovered on day 3 after drought stress.

Chlorophyll content decreased significantly in all populations on the 30th day of drought stress (Fig. 6). After rewatering, chlorophyll content was similar to that of the control treatments in Isparta and Çanakkale populations on the 3rd day and in other populations on the 10th day.

Discussion

Applying drought stress to different populations of *Q. cerris* across semi-arid, semi-humid, and humid climates revealed significant insights into their physiological responses, in terms of midday water potential, gas exchange parameters, total soluble sugar, and chlorophyll content. Drought stress significantly decreased midday water potential in seedlings from all

five populations. The interactions among populations, treatments, and sampling time were also significant for midday water potential. By the 30th day of drought stress, seedlings from different populations had varying reductions in midday water potential. Those of the Yozgat population, originated from a semi-arid climate, maintained a relatively higher midday water potential (-3.5 MPa) than those from other populations, whereas the Çanakkale seedlings, originated from a humid climate, exhibited a lower value (-4.5 MPa). A mean midday water potential of -4.7 MPa was reported

after 58 days of water deficit (Schimpl et al. 2019). Each species can adjust its physiological responses to environmental conditions under water deficit, and the degree of drought adaptation can vary significantly among genera and species (Time et al. 2018). By the end of the drought-recovery phase (R₃), the midday water potential of previously stressed plants reached values similar to those of control seedlings across all populations. Following re-watering, soil water content remained low, but leaf water status recovered.

Water shortage affects a wide range of

Tab. 2 - Effects of drought stress on physiological and biochemical characteristics. (T): sampling time; (P): populations; (D): drought stress; (TXP): interactive effect of sampling time and population; (PXD): interactive effect of populations and drought stress; (DXPXT): interactive effect of sampling time, population, and drought stress; (*): $P < 0.05$; (**): $P < 0.01$; (ns): non-significant.

Variables	F value						
	T	P	D	TXP	PXD	TXD	TXPXD
SWC	134.3**	1.9 ^{ns}	948.2**	0.8 ^{ns}	0.3 ^{ns}	94.8**	1.4 ^{ns}
Ψ_{md}	55.7**	5.2**	156.9**	6.8**	3.6**	42.4**	2.0*
A_{net}	175.4**	45.3**	906.6**	26.6**	14.8**	130.2**	36.1**
g_s	163.7**	187.6**	2509.4**	37.3**	117.7**	226.4**	47.8**
E	114.9**	13.8**	1909.3**	16.7**	11.7**	161.4**	32.1**
C_i	85.1**	21.0**	1.4 ^{ns}	10.8**	4.0**	23.9**	4.2**
TSC	4.8**	13.1 ^{ns}	6.0*	18.4**	1.2 ^{ns}	7.0**	1.7 ^{ns}
Chl	1.2 ^{ns}	3.8*	8.1*	1.3 ^{ns}	2.9*	4.3*	0.5 ^{ns}

plant characteristics and processes, including gas exchange (Peguero-Pina et al. 2018, Koç 2021, Sousa Leite et al. 2022), predawn and midday water potential (Deligöz & Bayar 2018, Atar et al. 2024). Stomatal management controls how much water plants take up and how long they can withstand drought stress (Time et al. 2018). *Anet*, *gs*, and *E* differed significantly in sampling time, population, drought stress, and their interactions. On the 30th day of drought stress, stomatal conductance approached zero. With increasing drought stress, a decrease in net photosynthetic rate and stomatal conductance has been reported in *Q. ilex* (Rodríguez-Calcerrada et al. 2018), *Q. cerris* (Deligöz & Bayar 2018), and *Q. brantii* Lindl (Jafarnia et al. 2018). During drought stress, early stomatal closure is typical of isohydric plants. In contrast, when water is scarce, anisohydric plants delay stomatal closure, allowing the leaf water potential to drop as soil water content declines (Tardieu & Simonneau 1998). Nine species showed this typical response, with a significant reduction in *Ci* during the early stomatal control phase, when stomatal conductance decreased. A substantial nonstomatal limiting phase was observed as *gs* dropped to low values, leading to a rise in *Ci* as *gs* approached a minimum (Brodribb 1996). In *Q. cerris* seedlings, *Ci* increased with drought stress. Since closed stomata keep CO₂ out of plant leaves, this may be the cause of the intercellular build-up of CO₂. However, because photosynthesis cannot proceed effectively without sufficient CO₂, the rate of photosynthesis can be low. Diffusion constraints on CO₂ uptake mostly limit photosynthesis until water stress reaches an extreme level at which practically no water remains for transpiration (Sun et al. 2014). Ying et al. (2015) found that the reductions in *gs*, *E*, and *Ci* under severe-stress conditions in the Kunming provenance were higher than those in the other populations, suggesting a better adaptation of that provenance to dry conditions. In this study, the decrease in net photosynthetic rate under stress in *Q. cerris* seedlings from Yozgat, Çanakkale, and Balıkesir populations was relatively greater than in Isparta and Sinop provenances. In seedlings from both these populations, *gs* and *Anet* declined dramatically following drought stress exposure, and there was a clear positive correlation between *Anet* and *gs* (Ma et al. 2014). The rates of transpiration, stomatal conductance, and *Anet* were found to be strongly positively correlated in *Q. cerris* seedlings. In drought-stressed oak seedlings, the net photosynthetic rate of all populations increased on the 3rd day after re-watering, but *Anet*, *gs*, and *E* fully recovered on the 3rd day after rewatering. This suggests that incomplete recovery of the net photosynthetic rate can be due to the persistence of stomatal limitations (Gori et al. 2023). Across all populations, *Anet* reached values comparable to those of the control

seedlings by the 10th day, at the end of the recovery period. Photosynthetic performance improved progressively during the re-watering period (Gallé et al. 2007). Previous studies demonstrated that drought-tolerant angiosperms have a rapid recovery of net photosynthetic rate after a few days of rewatering (Urli et al. 2013). *Anet* and leaf have been reported to recover to control levels 16 days after rehydration in *Bertholletia excelsa* (Schimpl et al. 2019).

Drought stress increased the total soluble sugar content and decreased chlorophyll content in *Q. cerris* seedlings. Total sugar accumulation in response to drought stress was observed in seedlings from all populations, except Sinop. Following rewatering, total sugar levels decreased rapidly. The concentration of soluble sugar increased as a result of the drought in *Pinus tabulaeformis* Carr. Re-watering dramatically reduced the content of leaf-soluble sugars under severe and moderate drought treatments (Guo et al. 2021). Sugar accumulation has been observed in *Quercus* seedlings grown under drought stress (Jafarnia et al. 2018, Atar et al. 2024). In this study, after three days of re-watering, the total soluble sugar content in all populations in the drought-stress treatments was nearly identical to that of the control. Chlorophyll content was affected by populations, drought stress, the populations × drought stress interaction, and the sampling time × drought stress interaction. Drought stress also affected leaf chlorophyll concentration. Chlorophyll content has been reported to decrease significantly in the leaves of two *Quercus* species as the duration of drought stress increased (Özden & Bayçu 2024). A considerable drop in chlorophyll content may indicate chlorophyll degradation caused by water deficit. In stressed *Q. cerris* plants, chlorophyll content steadily improved throughout the re-watering phase. Low water availability could reduce CO₂ concentrations inside the chloroplast due to stomatal closure, therefore the drop in photosynthetic pigment concentrations could help prevent serious damage to the photosynthetic apparatus. After a period of rewatering, chlorophyll levels were fully restored, accelerating the recovery of photosynthesis (Oliveira et al. 2014).

Provenances from higher altitudes have been reported to survive better to drought-stress than those from lower altitudes (Soto-Correa et al. 2015). The altitude of the Sinop population is the lowest among other populations of *Q. cerris* analyzed in this study. Compared with seedlings from drier climatic provenances, those from wetter provenances showed higher tolerance to drought stress (Jafarnia et al. 2018). In this study, the Yozgat population withstood drought by maintaining higher water potential, whereas seedlings from the Çanakkale population tolerated low water potential by increasing total soluble sugar content. This could be hy-

pothesized to be due to the severe summer drought occurring in Çanakkale, which was classified as humid climate site. Indeed, *Q. cerris* populations with a low summer drought index may be well adapted to dry conditions. Regarding leaf gas exchange, provenances from humid climate demonstrated the lowest resistance to water deficiency and the lowest capacity of recovery following rewatering (Pšidová et al. 2015). Alonso-Forn et al. (2021) noted that water stress applied gradually to Mediterranean oak species (*Q. faginea* Lam. and *Q. ilex* subsp. *rotundifolia* Lam.) exhibited different functional strategies to cope with water deficit. In addition, the evergreen species *Q. ilex*, with a less developed root system, likely maintains a lower net photosynthetic rate and leaf area than deciduous species. In contrast, deciduous European oaks such as *Q. robur* and *Q. petraea*, tend to adopt an avoidance strategy by establishing deep root systems to cope with drought stress (Früchtenicht et al. 2021).

Conclusions

This study highlights the significance of population-level variation in drought tolerance in *Q. cerris*, demonstrating how local climatic conditions can shape physiological and biochemical responses to drought stress. *Q. cerris* populations in Isparta, Balıkesir, Çanakkale, and Yozgat exhibited adaptive responses to drought, in terms of decreased midday water potential and gas exchange, along with increased total soluble sugar accumulation. While these findings support our initial hypothesis, they also suggest that drought tolerance may be more strongly associated with the severity of summer drought experienced by populations than with their classification as originating from semi-humid or humid regions. Our results underline the importance of identifying well-adapted populations for future afforestation and seed transfer programs, particularly in regions anticipated to experience drought as a consequence of climate change.

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Supplementary Material

Fig. S1 - Geographical distribution of section *Quercus cerris* L. and distribution of the populations (Yozgat, Isparta, Balıkesir, Çanakkale, and Sinop) in Turkey.

Fig. S2 - Schematic representation of irrigation-induced progressive drought (10, 20, and 30 days of drought) followed by recovery (3 and 10 days).

Fig. S3 - Principal component analysis of physiological and biochemical properties in treatments.

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